THE SEASONALITY OF FOUR ODONATA SPECIES FROM MID CANTERBURY, SOUTH ISLAND, NEW ZEALAND

A thesis

submitted in partial fulfilment

of the requirements for the Degree

of

Doctor of Philosophy in Zoology

in the

University of Canterbury

by

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1979

To Ann

ABSTRACT

Odonate seasonality is determined at Isaac's Pond (43°28'S; 172°32'E) 30 m amsl and at two sites at Lake Sarah (43°03'S; 171°47'E) 579 m amsl in New Zealand. The means by which seasonality is attained and the effects that altitudinal differences have on the pattern of seasonality is examined in field and laboratory studies.

Xanthocnemis zealandica (Coenagrionidae) has a two-year life cycle at Isaac's Pond, but a three-year life cycle at Lake Sarah - tb (*Typha* - bed site). Emergence starts earlier at Isaac's Pond, but ends by approximately the same date at all three sites. Emergence is trimodal at Isaac's Pond and bimodal at Lake Sarah. Embryonic development is direct; hatching occurs only the summer that eggs are laid. Later instar larvae cease development at about 7 - 9°C. Diapause, possibly cued by rate of change of daylength and temperature, occurs during the summer in the F-2 to F instar larvae.

Austrolestes colensonis (Lestidae) has a two-year life cycle at Lake Sarah - tb. Emergence starts earlier at Isaac's Pond, but ends by approximately the same date and is bimodal at all three sites. Embryonic development usually is direct, although some delayed hatching occurs. Some eggs hatch the summer that they are laid, but others overwinter and hatch the following spring. Supplementary moulting occurs in F-2 instar larvae during the summer.

Procordulia smithii (Corduliidae) has a four-year life cycle and a bimodal emergence pattern at Lake Sarah - tb. Embryonic development is direct above approximately 19°C, but greatly prolonged below this temperature; therefore, most eggs overwinter. Results from larval laboratory studies are tentative.

Procordulia grayi (Corduliidae) is examined only briefly at Lake Sarah - ls (lake shore site).

In general larval growth restrictions occur during the late summer that effectively prevent emergence during the autumn when successful reproduction is unlikely.

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1. INTRODUCTION

The study of the seasonal occurrence 'seasonality' of Odonata continues to attract the attention of researchers each year. The term 'seasonality' refers to the correlation of life histories with the seasons of the year. The following examples illustrate ways in which this is achieved by insects (see Corbet 1978).

Growth often follows seasonal temperature fluctuations and dormant stages, quiescence or diapause, may occur during a particular part of the year. Migration serves as an alternative to dormancy in some species. Seasonal growth and especially dormancy often results in the restriction of a particular life stage or stages to a specific time of the year.

Dormancy, therefore, plays an important role in seasonality. A rigid definition of the dormant stages is needed to avoid misunderstanding in referral to the Odonata. Quiescence is a condition of torpor or inactivity induced by low temperature and terminated by a rise in temperature. Diapause, however, is a physiological condition. It is characteristically an anticipatory response which is usually induced by photoperiod in the Odonata (Ingram & Jenner 1976a), although sometimes it is induced by temperature or diet in other Orders. Diapause is not terminated simply by temperatures becoming permissive for growth but requires a certain time to elapse and certain physiological requirements to be fulfilled before normal development is resumed.

Diapause at present, is poorly understood in the Odonata. It takes various forms and it affects various life stages from species to species; therefore, diapause is difficult to define clearly. Further research is needed before meaningful comparisons can be made with other Orders.

The seasonality of an odonate is often different from what is apparent to the casual observer. An example of this is seen in the emergence and occurrence of adults. The teneral adult usually requires a period away from the emergence/reproductive site for maturation. Once maturation is completed the adult returns to the emergence/reproductive site for mating. Because of this period away

from the emergence site, adults are first noticed only after emergence has been in progress for some time. Also, because of the longevity of the adult, four to eight weeks for some species, individuals are often evident long after emergence has been completed. Therefore, very little can be inferred about the actual period of emergence from observations on the appearance of adults. Only accurate, standardised observations on life histories can provide the precise details required to clarify the nature of seasonality displayed by the Odonata.

Before the early 1950's almost all the work on Odonata was largely restricted to taxonomy, morphology, or casual observations on life histories. Notable exceptions to this were the works of Balfour - Browne (1909) and Calvert (1929). They examined in detail the nature of growth and development of the larvae for several species of Odonata.

Corbet (1956c, 1957a, 1957b, 1957c) provided precise details on the life history and phenology (the times of seasonally recurring events during the life history) of several species of Odonata in Britain. He summarised the available literature (Corbet 1962) and indicated areas where further research was needed. This had a stimulatory effect on research in this field.

Most studies on the seasonality of Odonata have been carried out in Europe, North America, or Japan; whereas little work has been completed in Australasia, in particular, New Zealand. Up to 1950 the work on the Odonata of New Zealand centred around taxonomic problems, species distribution and species affinities, with an occasional reference to aspects of natural history as in Hudson (1892, 1904) and Tillyard (1912, 1920). Seasonality, as such, was not studied until Wolfe (1949, 1953) determined a life history for *Uropetala carovei* (White). Armstrong (1958a, 1958b) made casual observations on the duration of the egg stage of *Procordulia smithii* (White), *Procordulia grayi* (Selys) and *Hemicordulia australiae* (Rambur) and on the flight season of *Hemianax papuensis* (Burmeister). Scott (1963) determined the duration of the egg stage and the number of instars of *Xanthocnemis zealandica* (McLachlan) near Auckland. Crumpton (1975) described the adult behaviour and seasonal occurrence of *X. zealandica* and *Austrolestes colensonis* (White). Prestidge (1976) made observations on the duration of the egg stage and larval

development of *Aeshna brevistyla* Rambur and *H. australiae* but concentrated mainly on aspects of their feeding behaviour and energetics. Of the above, only the work of Wolfe (1949, 1953) provides a detailed account of the life history of one odonate species in New Zealand.

In New Zealand 11 species of Odonata from six families are recognised by Wise (1973). Of these, seven species are reported from Mid Canterbury (see Crosby, Dugdale & Watt 1976), South Island (Crumpton 1977; F. Kramer, Zoology Department, University of Canterbury, pers. comm. 1979).

ZYGOPTERA

Coenagrionidae:

(i) - *X. zealandica*

Lestidae:

(ii) - *A. colensonis*

ANISOPTERA

Corduliidae:

(iii) - *P. grayi*

(iv) - *P. smithii*

(v) - *H. australiae*

Petaluridae:

(vi) - *U. carovei*

Aeshnidae

(vii) - *A. brevistyla*

The first four species listed and *U. carovei* are endemic to New Zealand. The zygopterans are most abundant and are commonly found in ponds and lakes although they sometimes occur in sluggish streams (Crumpton 1977). The *Procordulia* spp. are less common, usually being restricted to mountain habitats or lowland areas undisturbed by man (Armstrong 1958a). *H. australiae* is rarely seen, the only record from Mid Canterbury that I am aware of was obtained by F. Kramer, Zoology Department, University of Canterbury, Christchurch on 7 February 1979. *U. carovei* is usually found in restricted areas of the mountains (Wolfe 1953). *A. brevistyla* is a species that is found throughout much of Australia (Watson 1974) and is probably a relatively recent arrival in New Zealand. It has been collected at Shipley's Large Pond (Crumpton 1977) and at Lake Sarah during this study but is seldom seen

in Mid Canterbury. This study deals with *X. zealandica*, *A. colensonis*, *P. smithii* and *P. grayi*.

New Zealand is located in a fairly high latitude but, because of maritime influences it enjoys a relatively mild climate. Local effects and unseasonable weather conditions are recognised as playing an important part in many natural ecosystems (Hurnard 1978). In Mid Canterbury the climate varies from mild and subhumid in the bottom lands to cold and superhumid in the mountains (Map 19, McLintock 1960).

During this study I attempted to determine the seasonality of *X. zealandica* in the egg and especially the larval stages and at emergence at two locations experiencing different climates. Most of the field and laboratory work was concentrated on this species in an effort, firstly to provide an accurate account of its pattern of seasonality and then to examine the effects that altitudinal differences, expressed as climatic differences, have on this pattern. The means of attaining seasonality were determined and the nature of diapause in this species was examined.

Less effort was concentrated on the remaining species. The seasonality of *A. colensonis*, in the egg and larval stages was determined at one location and the emergence pattern at two locations. Observations on the *Procordulia* species were carried out at one location. Egg, larval and emergence studies were made on *P. smithii* and emergence studies only were made on *P. grayi*. The means by which seasonality was attained in these species and the nature of their diapause (if any) was examined, but in less detail than was the case for *X. zealandica*.

2. SYSTEMATICS

The classification of the dragonfly fauna of New Zealand was reviewed by Wise (1973) who followed the modified Fraser (1957) classification after O'Farrell (1970). Wise made one taxonomic correction from previous works. The combination *Austrolestes colensonis* (White) (family Lestidae, subfamily Sympecmatinae) replaced that of *Lestes (Indolestes) colensonis* (White), which previously had been listed incorrectly in the family Sympecmatidae by Wise (1965) and Penniket (1966). The corrected classification as presented by Wise (1973) is used in this study.

I collected adults and larvae from various areas in an initial survey to determine odonate abundance and to select suitable study sites. Specimens were identified on the basis of characters presented by Armstrong (1958a), Wise (1962) and Penniket (1966). Four species, *X. zealandica*, *A. colensonis*, *P. smithii* and *P. grayi* were chosen for study and two study areas, Isaac's Pond and Lake Sarah were selected. Larvae of these species were the only odonates encountered in the aquatic habitats at these sites. A key (Table 1) for species identification of the larval stages, including exuviae, of the four species was designed for use in the field studies and characteristics were determined for the recognition of various larval instars of *X. zealandica*, *A. colensonis* and *P. smithii* (Tables 2 to 4) for use in the laboratory studies.

The terminology used for the labium is that of Corbet (1953) and Wise (1962). The two zygopterans could be identified easily on the basis of family characteristics in the later instars. Earlier instars, occasionally had to be mounted on slides for examination of their mouthparts. A Wild M5 Dissecting Microscope equipped with an ocular grid and a transmitted-light stand (bright and dark field) illumination source was used at a magnification of 200X. The characters of the labial palpus proved definitive for species separation throughout the larval stages.

The two *Procordulia* species could be identified in the second, and the mid-to final instars; however, larvae with a head width from about 0.46 to 1.50mm, representing the third to approximately the

sixth instars, could not be positively identified to species. Second instar larvae were mounted on slides and examined as described for the zygopteran species. The body setae of the third instar are similar for both species and the tubercles on the head, which are present on all the *P. grayi* larvae examined, are also present on some of the *P. smithii* by this stage. Not until larvae attained a head width of about 1.50mm, the stage at which wing pads first became apparent, could specimens be separated positively by means of the number of setae on the labial palpus and the presence or absence of middorsal hooks on the abdomen. The body shape and prominence of the eyes were not definitive characters but they proved useful for initial grouping of specimens for subsequent species identifications.

For instar separation morphological measurements were made of body structures that were not appreciably altered in size by preservation. Therefore, measurements could be made on both live and preserved material with comparable results. Head width was measured through the eyes, across the widest portion of the head. Metathoracic wing pad length was measured along the medial margin, from the base to the apex. Measurements were made using a Wild M5 microscope, as described earlier, at a magnification of 25X.

No attempt was made to separate all the instars of each species as the number of instars of most odonate species appears not to be fixed. Balfour - Browne (1909) first noted this phenomenon in the Odonata. He found that *Agrion pulchellum* Lind. transformed to the adult stage after 11 to 14 instars, including the pronymph. Later Calvert (1929) found that two of the three larvae of *Nannothemis bella* (Ubler), reared in the laboratory from the egg stage, reached the adult stage after 12 instars. The third larva required 13 instars to complete development. Gardner (1951) noted that in some species, members of the same egg batch required several extra moults to complete development. Schaller and Mouze (1970) and Ingram and Jenner (1976a) have since demonstrated supplementary or reduced moulting in several species, caused by various genetic and environmental factors.

Only very early and the later instars can be separated with any degree of confidence; therefore, only the second and the final (F), penultimate (F-1) and antipenultimate (F-2) instars were characterised

for this study. The characteristics presented in Tables 2 to 4 proved adequate for the separation of most specimens into the appropriate instars. A few late instar larvae could not be definitely assigned to a specific instar. When necessary these individuals were reared in the laboratory to obtain a definite instar identification.

In section 4.2.2. approximate instars were assigned to early instar larvae. The reasoning for this is explained in that section.

TABLE 1. Key to species of larvae.

1a. Larvae slender; abdomen not widening from the base; end of abdomen with three caudal lamellae (sometimes fewer if lost in handling) ZYGOPTERA 2

1b. Larvae stout; abdomen widening from the base; end of abdomen without caudal lamellae but with stiff, pointed appendages instead. ANISOPTERA
CORDULIIDAE
Procordulia 3

2a. All instars with end hook, notch, truncate lobe with at least three dentations, and movable hook on distal margin of labial palpus (Fig. 1). Later instars with labial palpus not deeply incised (Fig. 2); basal half of the prementum not greatly narrowed; prementum entire; caudal lamellae acuminate at apex with main tracheal branches at acute angles to the long axis of the lamellae; posterolateral margin of the head obtusely angular, body and legs relatively robust. COENAGRIONIDAE
Xanthocnemis zealandica
Instar recognition - Table 2

2b. All instars without the combination of end hook, notch, and truncate lobe with dentations on the distal margin of the labial palpus. Early instars with reduced end hook, distal margin serrate and movable hook only, on labial palpus (Fig. 3). Later instars with labial palpus deeply incised and intermediate hooks present (Fig. 4); basal half of the prementum greatly narrowed; prementum cleft; caudal lamellae broadly rounded at apex with main tracheal branches at right angles to the long axis of the lamellae; posterolateral margins of the head broadly rounded; body and legs slender, fragile. LESTIDAE
Austrolestes colensonis
Instar recognition - Table 3

3a. Larvae small (second instar); head width 0.36 to 0.46mm; 1 seta on labial palpus. 4

3b. Larvae larger; head width about 1.50mm or larger; wing pads present as tiny bumps or larger. 5

4a. Setate tubercle present on dorsum of the head, posteromesal to the posterior margin of the eye; body setae fleshy (Fig. 5). *Procordulia grayi*

4b. No tubercles present on dorsum of head, small setae only present; body setae normal (Fig. 7). *Procordulia smithii*

Instar recognition - Table 4

5a. Setae on labial palpus never more than 4; no middorsal hooks present on surface of abdomen; body shape and eyes as in Fig. 6. *Procordulia grayi*

5b. Setae on labial palpus 5 or 6; middorsal hooks on abdomen small and blunt in early instars, becoming large and pointed in later instars; body shape and eyes as in Fig. 8. *Procordulia smithii*

Fig. 1. Prementum and labial palps of a second instar *Xanthocnemis zealandica* larva, dorsal view.

Fig. 2. Right labial palpus of a final instar *Xanthocenmis zealandica* larva, dorsal view.

Fig. 3. Prementum and labial palps of a second instar *Austrolestes colensonis* larva, dorsal view.

Fig. 4. Right labial palpus of a final instar *Austrolestes colensonis* larva, dorsal view.

Abbreviations to Figs. 1-4

D - dentations
EH - end hook
IH - intermediate hooks
LP - labial palpus
MH - movable hook
N - notch
P - prementum
PS - palpal seta(e)
S - serrations
TL - truncate lobe

Fig. 5. Second instar larva of *Procordulia grayi*, dorsal view. Legs and antennae omitted.

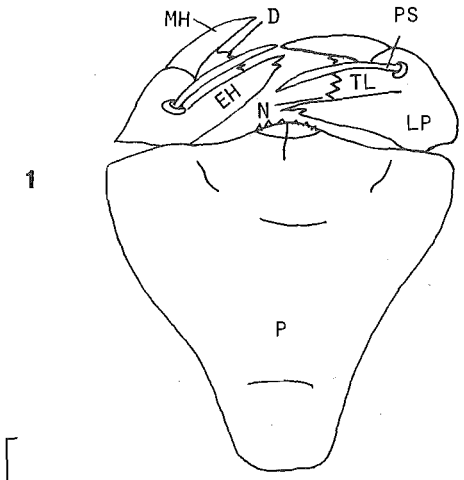
Fig. 6. Mid-instar larva of *Procordulia grayi*, dorsal view. Legs and antennae omitted.

Fig. 7. Second instar larva of *Procordulia smithii*, dorsal view. Legs and antennae omitted.

Fig. 8. Mid-instar larva of *Procordulia smithii*, dorsal view. Legs and antennae omitted.

Abbreviations to Figs. 5-8

AA - anal appendages
E - Compound eye
FS - fleshy setae
MH - middorsal hooks
NS - normal setae
ST - setate tubercle
WP - wing pads



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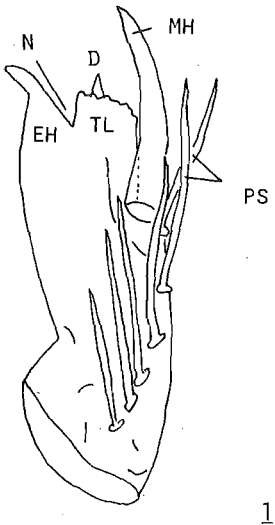

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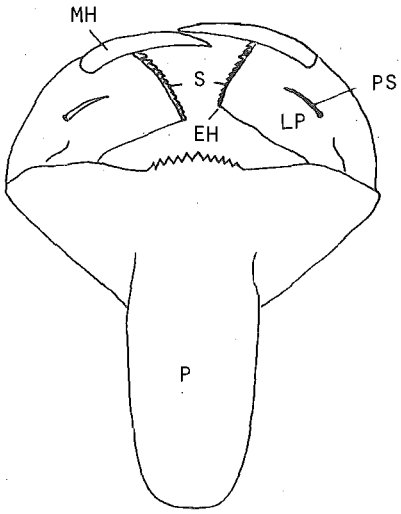

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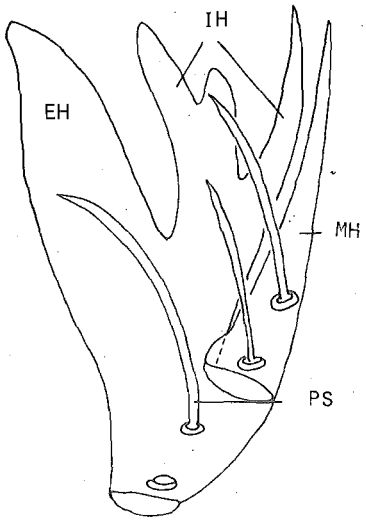

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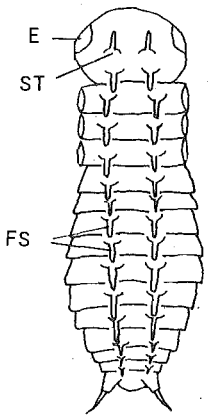

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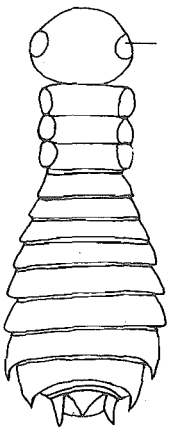

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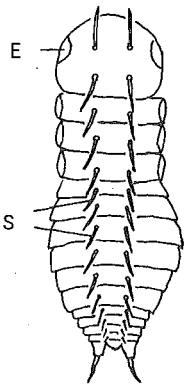

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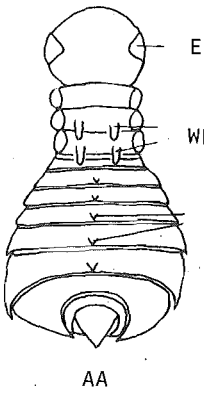

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Tables 2 to 4. Characters for the recognition of some larval instars of *Xanthocnemis zealandica*, *Austrolestes colensonis*, and *Procordulia smithii*. The maximum and minimum values of measurements made throughout the year are presented. For measurement techniques refer to the text.

TABLE 2. *Xanthocnemis zealandica*

Instar	Head Width (mm)	Wing Pad Length (mm)	Remarks
Second	0.30 - 0.34	-	No premental setae, 1&1 palpal setae
F-2	2.20 - 2.56	1.04 - 1.44	
F-1	2.68 - 3.00	1.84 - 2.32	
F	3.20 - 3.52	3.60 - 4.08	

TABLE 3. *Austrolestes colensonis*

Instar	Head Width (mm)	Wing Pad Length (mm)	Remarks
Second	0.32 - 0.36	-	No premental setae, 1&1 palpal setae
F-2	3.12 - 3.60	1.60 - 2.16	
F-1	3.52 - 4.00	2.20 - 2.80	
F	4.00 - 4.48	4.93 - 5.87	

TABLE 4. *Procordulia smithii*

Instar	Head Width (mm)	Wing Pad Length (mm)	Remarks
Second	0.36 - 0.42	-	1&1 palpal setae
F-2	3.28 - 3.76	1.60 - 1.78	
F-1	4.28 - 4.80	3.16 - 3.40	
F	5.80 - 6.30	4.85 - 6.72	

3. STUDY AREAS

3.1. GENERAL

As mentioned, work was carried out at two locations (Fig. 9) in Mid Canterbury. Isaac's Pond is situated on the Canterbury Plains, whereas Lake Sarah is situated in the Southern Alps. These areas were chosen for the following reasons:

- adequate populations of Odonata were present for study purposes; and
- the two locations experienced different climates.

Air and water temperature, photoperiod and chemical conditions were examined at the study areas.

3.2. STUDY AREA DESCRIPTION

3.2.1. Isaac's Pond

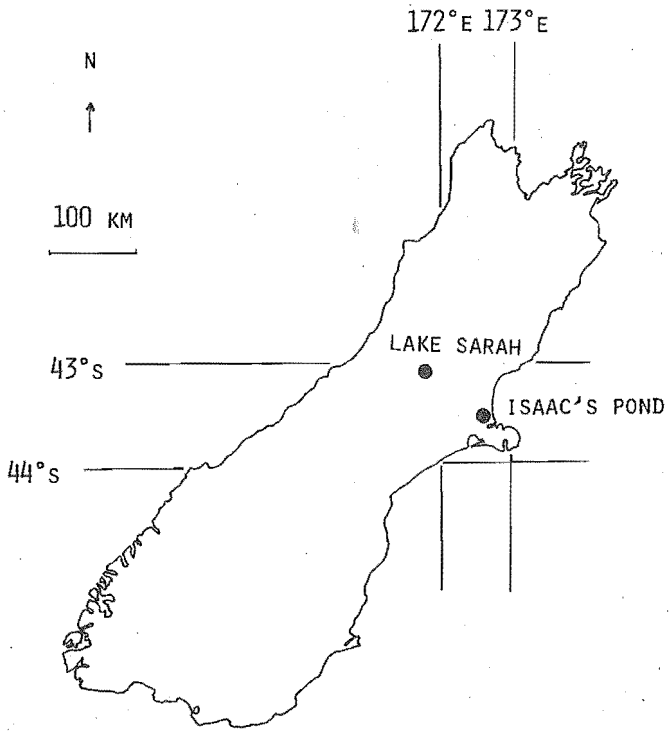
3.2.1.1. 'Isaac's Pond site' Isaac's Pond is situated at, 43° 28'S; 172° 32'E; (NZMS 1 S76 910637) at an altitude of about 30m above mean sea level, about 2.0km NW of the Christchurch International Airport. It is a man-made pond in a disused portion of a shingle pit owned by "The Isaac Shingle and Sand Co. Ltd.". The gravel was deposited in this area by the Waimakariri River, probably during the late Pleistocene (Gage 1969). The pond was made in 1968 when a drag line was used to form a series of channels and ponds by excavating to below the water level. Artesian water, derived from rain on the Canterbury Plains or possibly, as leakage from the rivers (Gage 1969), flows slowly through the channels at Isaac's Ponds and empties into the South Branch of the Waimakariri River.

Observations were made from August 1975 to August 1978 in the south channel only of Isaac's Pond (Fig. 10). Regular collections of larvae and exuviae were made, and air and water temperatures were recorded. The channel is 120m long with a minimum width of 14m and a maximum width of 17m. The bottom of the channel slopes steeply to a maximum depth of about 3.0m in the centre.

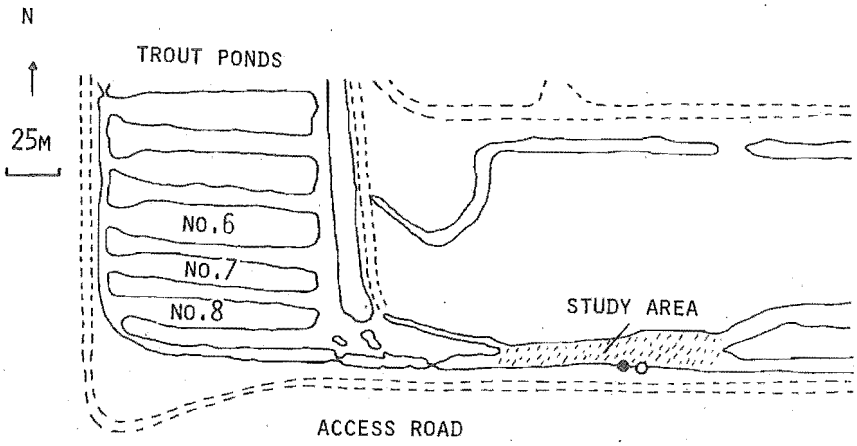
Fig. 9. South Island, New Zealand, study area localities mentioned in text.

Fig. 10. Isaac's Pond study area. Hollow symbol - exuviae collection site; solid symbol - temperature recorder.

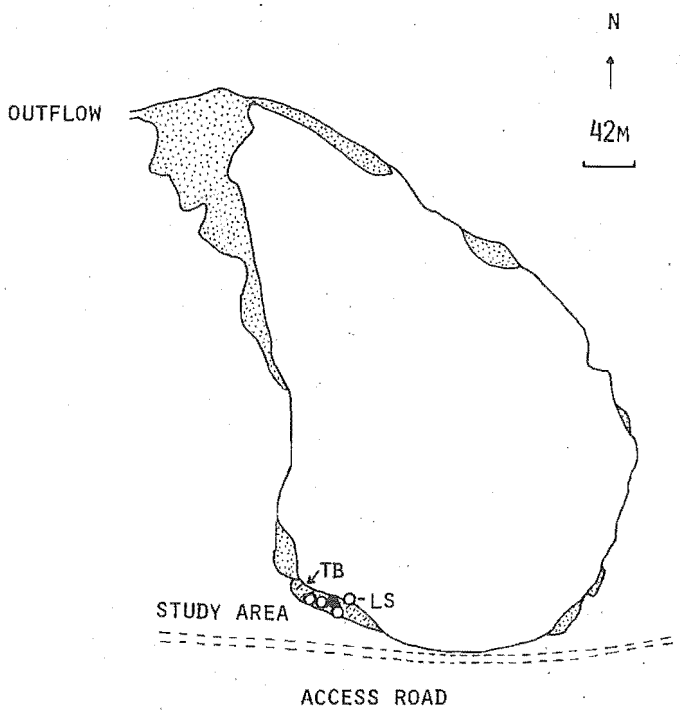
Fig. 11. Lake Sarah study area with Lake Sarah - tb and Lake Sarah - ls sites indicated. Hollow symbol - exuviae collection site; solid symbol - temperature recorder; stippled area - *Typha orientalis*.


172°E 173°E
N
100 KM
43°S
LAKE SARAH
ISAAC'S POND
44°S

9


N
TROUT PONDS
25M
NO.6
NO.7
NO.8
STUDY AREA
ACCESS ROAD

10


N
OUTFLOW
42M
TB
LS
STUDY AREA
ACCESS ROAD

11

During this study the submerged aquatic vegetation was made up almost entirely of *Elodea canadensis* Rich. with small intermixed patches of *Myriophyllum* sp. . This vegetation was occasionally covered by a thick mat formed by *Spirogyra* sp. . The marginal vegetation extending into the water was almost exclusively *Juncus gregiflorus* Johnson.

3.2.1.2. Climate Isaac's Pond lies within the 'Eastern South Island' climatic region of Garnier (1958) which is characterised by the following:

- 'Easterly' influences are the dominant ones, being expressed particularly in a high variability of rainfall, and relatively large mean annual ranges of temperature;
- Antarctic influences are particularly marked in the area from time to time; and
- It is a generally homogeneous climatic unit.

Because of local effects at Isaac's Pond the climate deviates slightly from the above general characters. The proximity of the ocean, about 15km, reduces the number of days of ground frosts observed and accentuates the influences of "Easterly" winds. As a general rule the "North-Westerly" winds at the surface are experienced more frequently in inland 'Eastern South Island' and reach only to within about 35-40km of the east coast (Garnier 1958). With more 'Easterly' winds there is a smaller range of mean annual temperatures at Isaac's Pond.

Rainfall in this area is experienced as a primary winter maximum and a secondary summer maximum because the Banks Peninsula, which rises to over 500m above mean sea level, promotes orographic lifting of the air. The rest of the 'Eastern South Island' area has a summer maximum in rainfall (Garnier 1958). The annual rainfall totals at Isaac's Pond are as variable as in the rest of the 'Eastern South Island' area.

3.2.2. Lake Sarah

Lake Sarah is situated at, 43° 03'S; 171° 47'E; (NZMS 1 S66 245158) at an altitude of about 579m above mean sea level, about 154km NW of the Christchurch International Airport. It is of glacial and alluvial origin, existing probably continuously since the Poulter advance about 17-13 x 10^3 years ago (Gage 1959). Three sides are

enclosed by ablation moraine and other glacial deposits, whereas the west side is bounded by a small salient of the Cass River alluvial fan. A small outlet stream is situated at the northern tip of the lake. There are no streams that feed directly into the lake, inflow occurs as seepage from the surrounding tussock catchment.

Observations were made from February 1976 to April 1978 at two sites, one in a *Typha* - bed and the other along the shore of the lake.

3.2.2.1. '*Typha* - bed site' This site is hereafter referred to as Lake Sarah - tb. The bed of *Typha orientalis* Presl at the southern end of the lake, closest to the access road (Fig. 11), comprised the principal study site at Lake Sarah, from which regular collections of larvae and exuviae were made and at which temperature records for the water and air were taken. Lake Sarah - tb varies from about 10 to 15m wide and is about 85m long. The site is separated from the lake by a floating raft of *T. orientalis* rhizomes overgrown by grasses and *Schoenus pauciflorus* (Hook) which forms a margin from 1.0 to 3.0m wide. This margin restricts water movement between the areas to a slow seepage. Within Lake Sarah - tb the water is shallow, in the form of interconnected pools, with a maximum depth of about 1.0m.

The bottom is composed of a thick layer of decaying organic matter, derived mainly from *T. orientalis*. Little submerged aquatic vegetation was present during this study; the emergent vegetation made up most of the flora. This was a combination of *Juncus articulatus* L., humps of *Carex goyenii* Petrie, and *T. orientalis* with the latter species predominant.

3.2.2.2. 'Lake-shore site' This auxillary site at Lake Sarah is hereafter referred to as Lake Sarah - ls. Collections of exuviae only were made from this site on the south shore of the lake (Fig. 11) adjacent to Lake Sarah - tb. Lake Sarah - ls consisted of a 1.0m wide by 7.0m long strip of vegetation (mainly *S. pauciflorus*) growing on the floating raft of *T. orientalis* rhizomes. The lake has a maximum depth of about 6.7m and occupies an area of approximately 0.20km^2 (Stout 1977).

The aquatic vegetation was listed by Flint (1938). Since Flint's work *E. canadensis* has become the dominant macrophyte on the

bottom of the southern portion of the lake.

3.2.2.3. Climate Lake Sarah lies within the 'Upland South Island' climatic region of Garnier (1958) which is characterised by the following:

- 'Westerly' influences are the dominant ones being expressed particularly in plentiful and reliable rainfall, and relatively small mean annual ranges of temperature;
- Antarctic influences are particularly marked in the area from time to time;
- Effects of elevation within the region are marked, and expressed especially in cold winters and high rainfall totals; and
- It has a considerable diversity of climatic types.

The above general characters are supported, at least in part, by meteorological observations made at Cass Field Station which is situated about 2.2km NW of Lake Sarah. 'North-Westerly' winds occur 51% of the time at Cass (Greenland 1977). Although 'Westerly = North-Westerly' influences are dominant, the variability of mean annual rainfall is relatively high, about 14.9% (Greenland 1977). Both Cass and Lake Sarah lie in an area of steep annual rainfall gradient, between high values in the west and low values in the east. Maximum rainfall occurs during the spring, especially November, whereas the minimum rainfall occurs from February to May.

High summer temperatures, and relatively mild winter temperatures are characteristic of the macro-climate at Cass (Greenland 1977). The absolute maximum and minimum air temperatures recorded at the Cass Field Station are 37 and -16°C, respectively. Snow on the ground occurs for only a few days during the winter as the 'North-Westerly' winds actually serve to moderate the winter temperature in the area.

The timber-line is an expression of the overall effect of temperature, rainfall, wind and various other factors limiting tree growth. At Cass the timber-line, before Polynesian fires, lay at 1250 to 1280m (Burrows 1977). For comparison, on the west coast of North America at 48°N the timber-line on the Rocky Mountains lies at 3500m. On the east coast of North America at 39°N it lies at 2000m

on Mt. Rainier (Mani 1962).

The climate at Cass and Lake Sarah is one of the many variations found within the 'Upland South Island' climatic region. The effect of wind appears to be the dominant factor controlling the climate experienced. Winds at Cass are almost constant with a reported average annual wind speed of 4.9m ~ sec^{-1}, based on two years observations (Greenland 1977).

3.3. PHYSICAL AND CHEMICAL CONDITIONS

3.3.1. Introduction

The physical conditions, temperature and photoperiod were followed closely at both study areas as these two factors were considered to have the greatest potential for affecting the growth and development of the aquatic larvae. The seasonal change of temperature dictates the period during which growth and development occurs, whereas photoperiod is often involved in the induction and timing of diapause; although temperature is of major importance in modifying responses.

The chemical conditions that were considered to have the greatest potential for affecting growth and development of larvae were oxygen concentration and pH. Although little is known about the effect of minor fluctuations in the chemical conditions, it is known that Odonata larvae are relatively tolerant of changes. Swain *et al.* (1977) found that in *Anax* sp. the respiratory frequency increased and amplitude decreased with decreasing oxygen concentrations. When the oxygen concentration fell to 68% of saturation a change from a unimodal respiratory pattern to a bimodal pattern with a slight secondary inspiration and expiration peak was observed. This bimodal pattern is perhaps an indication that the animal began to react to stress at a level of about 68% of saturation. The bimodal pattern continued until respiratory failure, which occurred at 26% of saturation. Gaufin *et al.* (1974), working on several stream insects, found that the damselflies tested had the highest tolerance of low oxygen concentrations.

The effect of low pH on the stream species *Ophiogomphus rupinsulensis* (Walsh) and *Boyeria vinosa* (Say) was examined by Bell (1971). He found that 50% of the animals tested died after 30 days

exposure to a pH of 4.30 and 4.42, respectively. During emergence they were more susceptible to low pH and both species showed 50% mortality at a pH of 5.2.

Chemical conditions have been well documented for areas of Isaac's Pond (Teirney 1971; Field-Dodgson 1972) and for Lake Sarah (Flint 1938; Stout 1969). The extremes in oxygen concentration and pH, as found in these studies, did not approach the levels determined critical for various odonates by Swain *et al.* (1974) and Bell (1971). No chemical measurements were made during this study at Isaac's Pond or Lake Sarah. However, the fluctuation of the water level was noted to provide an indication of gross changes in the aquatic environment. Barclay (1966) found that anaerobic conditions occurred in a temporary pond, shortly before it dried out. Therefore, the water level fluctuations showed when the sites dried out, if at all, and provided information about the periods when anaerobic conditions were experienced, particularly at Isaac's Pond and Lake Sarah - tb.

3.3.2. Temperature

The air temperature was measured about 0.3m above the water surface in an area amongst the emergent vegetation where larvae were noted emerging and *A. colensonis* oviposited. Water temperature was measured about 0.2m below the water surface to obtain the aquatic temperature regimen experienced by the larvae. Mercury bulb maximum-minimum thermometers, screened from direct solar radiation by a protective tube of aluminium foil, were placed in the above mentioned positions and records to the nearest 0.5°C were made at each visit to the study site. The maximum-minimum indicators were then reset to the ambient temperature. Weekly maximum-minimum records were used to calculate mean monthly air and water temperatures. Two Foxboro continuous temperature recorders, one at Isaac's Pond and one at Lake Sarah - tb, were used to obtain the diel fluctuations of air and water temperature during the period at the start of adult emergence. The temperature probes were screened from direct solar radiation by cones of aluminium foil and positioned alongside the maximum-minimum thermometers at the study site.

All the temperature measuring devices were calibrated over the range of temperatures experienced in the field using a Messgeräte - Werk Lauda/Tauber K2R water bath (control accuracy: 0.01 to 0.03°C) against reference thermometer No. 1.25 (scale: -30 to 100 in 0.5°C).

Calibrations were made before placing and after removing the equipment from the field to ensure accurate readings. The readings obtained were adjusted according to the calibrations.

3.3.2.1. Isaac's Pond The location of the temperature recording equipment at Isaac's Pond is indicated on Fig. 10. Air temperature was measured in a dense clump of *J. gregiflorus* along the margin of the channel. The mean monthly air and water temperatures are shown in Fig. 12.

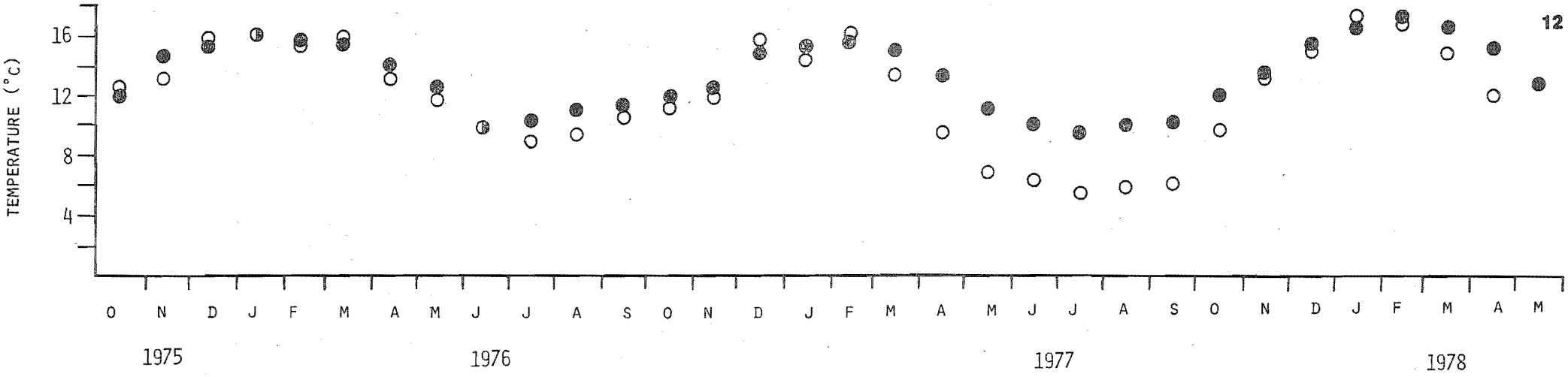
Each year the mean monthly air and water temperatures were similar, about 15± 1°C, during the period from December to February, the warmest months of the year. However, during the period March to November there was a noticeable difference between air and water temperatures, especially during 1977. The mean monthly air temperature was higher from March to November in 1976 than in 1977. As an example, the minimum mean monthly air temperature was 8.8°C in 1976 but 5.5°C in 1977. Although the mean monthly air temperature differed markedly from year to year, that of the water differed only slightly. The minimum mean monthly water temperature was 10.0°C in 1976 and 9.5°C in 1977. The local climate and the artesian water source at Isaac's Pond probably served to moderate the temperatures experienced, especially those of the water.

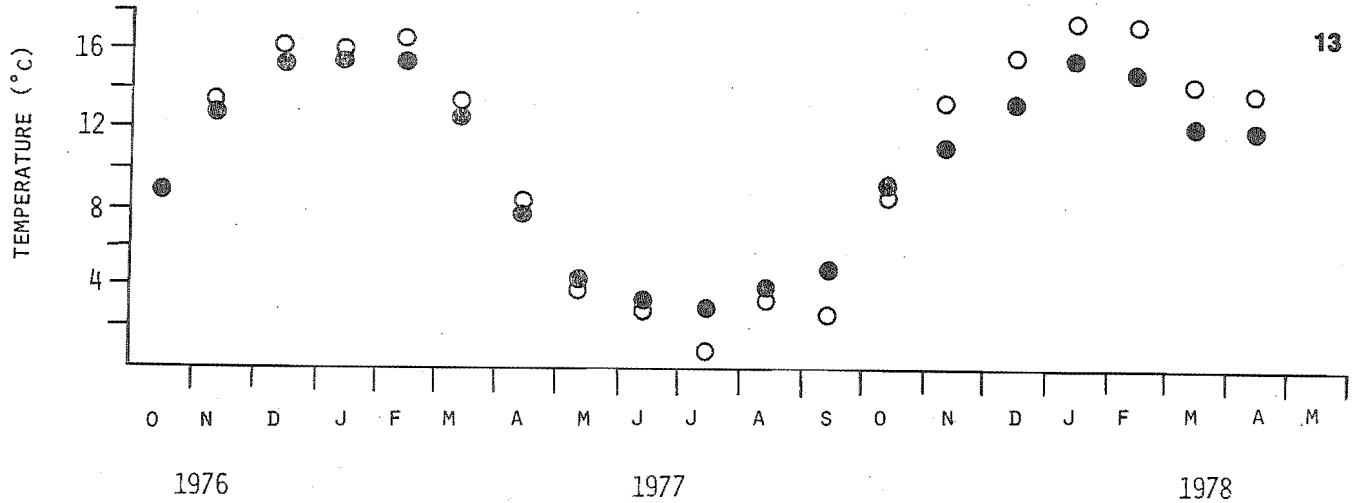
Shipley's Large Pond, located about 2.3km east of Isaac's Pond, probably has the same artesian water source as Isaac's Pond. Crumpton (1978) noted that during the summer Shipley's Large Pond experienced water temperatures (taken at 0.15 to 0.20m below the surface) lower than those experienced at a small pond located near the coast about 20km north of Christchurch. She found the annual range of water temperature, taken at the same depth as the above, was 6 to 26°C at this latter pond, whereas at Shipley's Large Pond the range was 5 to 22°C. At Isaac's Pond the range of water temperatures for the three years of this study, taken at 0.20mm, was 7 to 21°C, indicating the greatest degree of temperature moderation of these three ponds, probably because Isaac's Pond is a relatively large body of slow moving water with an artesian source.

Daily temperature fluctuation of the water also reflects a high degree of moderation at Isaac's Pond.

Fig. 12. Mean monthly air and water temperatures at Isaac's Pond from 1975 to 1978. Hollow symbols - air temperature; solid symbols - water temperature.

Fig. 13. Mean monthly air and water temperatures at Lake Sarah - tb from 1976 to 1978. Hollow symbols - air temperature; solid symbols - water temperature.


TEMPERATURE (°C)
16
12
8
4
O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M
1975
1976
1977
1978
12


TEMPERATURE (°C)
16
12
8
4
O N D J F M A M J J A S O N D J F M A M
1976
1977
1978
13

From continuous water temperature records at the study site, I found the maximum fluctuation to be about 5°C in one 24-hour period and the usual fluctuation was about 2 to 3°C. For comparison, Barclay (1966) found the average fluctuation per day to be 8°C in a temporary pond located near Auckland. She also found that on calm, clear days with cold, early morning temperatures a thermal stratification sometimes occurred with a difference of as much as 8.5°C between the surface and the bottom (0.35m). This indicates that the temperature regimen experienced at Isaac's Pond is perhaps more characteristic of a spring than of a pond.

The mean monthly water temperatures (Fig. 12) show that conditions were similar during December to January in the three years of this study. During 1977-1978 temperatures were slightly higher and during 1976-1977 temperatures were slightly lower than those experienced during 1975-1976. The temperatures throughout June to August were also similar from year to year, although as mentioned earlier in this section, conditions in 1976 were slightly warmer than those experienced in 1977. Warming took place at a relatively high rate from October to November. During this period temperatures rose most rapidly in 1975 and least rapidly in 1976. Warm weather continued well into April of 1978, whereas in both 1976 and 1977, March marked the end of the warm period. The mean monthly water temperature calculated for April 1978 was almost 2°C higher than those for April of 1976 or 1977.

3.3.2.2. Lake Sarah Detailed temperature records were made for Lake Sarah - tb only. The location of the temperature recording equipment is indicated in Fig. 11. Air temperature was measured amongst a dense clump of *T. orientalis*. The mean monthly air and water temperatures are shown in Fig. 13.

The temperature regimen experienced at Lake Sarah - tb was markedly different from that found at Isaac's Pond. From November to April the mean monthly air temperature consistently exceeded that of the water and from May to October the mean monthly water temperature exceeded that of the air, but only slightly. During the period from December to February, the warmest months of the year, the mean monthly water temperature was about 15± 1°C except for December 1977 when the mean value was 13.4°C. During the period from June to August, the

coldest months of the year, the mean monthly water temperature was about 4.0°C. Occasionally a thin layer of ice formed for a short time on the surface of the water in the *Typha* - bed. The range of water temperature for the two years that observations were made at Lake Sarah - tb was 1 to 23°C. Temperatures may have been moderated by seepage from the surrounding tussock.

From continuous temperature records at the study site, I found the maximum diel fluctuation to be about 6°C, although usually temperature varied by only 2 or 3°C per day. This, combined with the above observations, shows: - firstly that the temperature regimen experienced at Lake Sarah - tb is characteristic of a shallow body of water, 'pond'; and - secondly that the climate at Lake Sarah is more severe than that at Isaac's Pond. At Lake Sarah the summer is shorter and possibly warmer and the winter is longer and cooler than at Isaac's Pond.

Mean monthly water temperatures recorded at Lake Sarah - tb (Fig. 13) show that conditions were cooler during November and December in 1977 than in 1976, but similar during January and February. Warm weather continued through to April in 1978, whereas cold conditions were already prevalent by April in 1977.

Although detailed temperature records were made for Lake Sarah -tb only, some information was obtained on the temperature regimen experienced at Lake Sarah - ls. The water temperatures were recorded from early July 1977 to late April 1978, during which period a range of 4 to 20°C was found.

Flint (1938) during 18 months of observations at Lake Sarah, recorded a water temperature range of 4 to 21°C near the surface. This is considerably less than that experienced in Lake Sarah - tb, probably because Lake Sarah - ls has a much larger volume of water and therefore, the annual temperature range is moderated. This large volume of water also serves to dampen the daily fluctuation of water temperature. Stout (1977) noted that the shallow lakes in the Cass area, including Lake Sarah, are exposed to strong winds which almost continually mix the water and usually prevent thermal stratification. The continual wind action ensures that the water temperature of the entire lake follows the ambient air temperature. During prolonged periods of relatively constant air temperature and strong winds

Lake Sarah - ls and Lake Sarah - tb experience similar water temperature regimens.

3.3.3. Photoperiod

All time notations in this study are based on Solar Time (such that the elevation of the sun is highest at 1200 hours). Photoperiod regimens are presented as a proportion of hours of light to hours of dark. For example, 14L:10D denotes 14 hours of light to 10 hours of dark in one 24-hour cycle. The daylength 'photophase' in these notations is taken to consist of the period from the start of Civil Twilight in the morning to the end of Civil Twilight in the evening. Evening Civil Twilight is defined as the time required for the upper limb of the sun to traverse an arc from the horizon to a point lying 6° below the horizon (Beck 1968).

The daylength was designated to include the Civil Twilight periods because some insects are known to respond to the light intensities experienced then. The light intensity at the start and end of morning and evening Civil Twilight, respectively, is about 3.55 lux under clear conditions (Beck 1968). One lux is equivalent to 0.093 foot-candles or 4 ergs cm^{-2} sec^{-1} at a wavelength of 555mμ (Beck 1968). Saunders (1976) noted that the light intensity at which an insect shows a photoperiodic response is usually related to habitat. For example, Kogure (1933) found that the eggs and larvae of the silkworm moth *Bombyx mori* L. responded to light intensities of 0.1 to 0.8 lux and Paris and Jenner (1959) found that the larvae of the pitcher plant midge, *Metriocnemus knabi* Coq. responded to 0.025 lux. However, larvae of the oriental fruit moth, *Grapholitha molesta* (Busck) whilst burrowing in young apples, required a light intensity of 10 to 30 lux before responding (Dickson 1949).

Lutz and Jenner (1964), in work using Odonata, found that larvae of *Tetragoneuria cynosura* (Say) responded to a light intensity of at least as low as 0.03 lux and suggested that the threshold intensity for a photoperiodic response could be below 0.002 lux.

The daylengths for Isaac's Pond were considered to be identical to those for Christchurch International Airport. Tables for the beginning of morning Civil Twilight and the end of evening Civil Twilight in the Aeronautical Information Publication New Zealand (Ministry of Transport, Civil Aviation Division, Wellington) provided

the daylengths for Christchurch International Airport. The daylengths for Lake Sarah were provided by John Gilmour, Department of Physics, University of Canterbury, Christchurch. Fig. 14 shows the daylengths for the seventh and twenty-first day of each month during 1977 at Lake Sarah. The photoperiod regimen experienced at Isaac's Pond and Lake Sarah are almost indentical with a maximum difference of about six minutes less daylength at Lake Sarah at the summer solstice. The duration of the longest day at Lake Sarah was 16h 33min and that of the shortest was 10h 04min.

Most of the laboratory experiments using artificial photoperiods dealt with animals from Lake Sarah collected during 1977. The artificial photoperiodsused in the laboratory correspond to daylengths at Lake Sarah as follows:

- 16L : 8D, on 19 January and 24 November; and
- 10L : 14D, slightly shorter photophase than 21 June, the shortest day of the year (see Fig. 14).

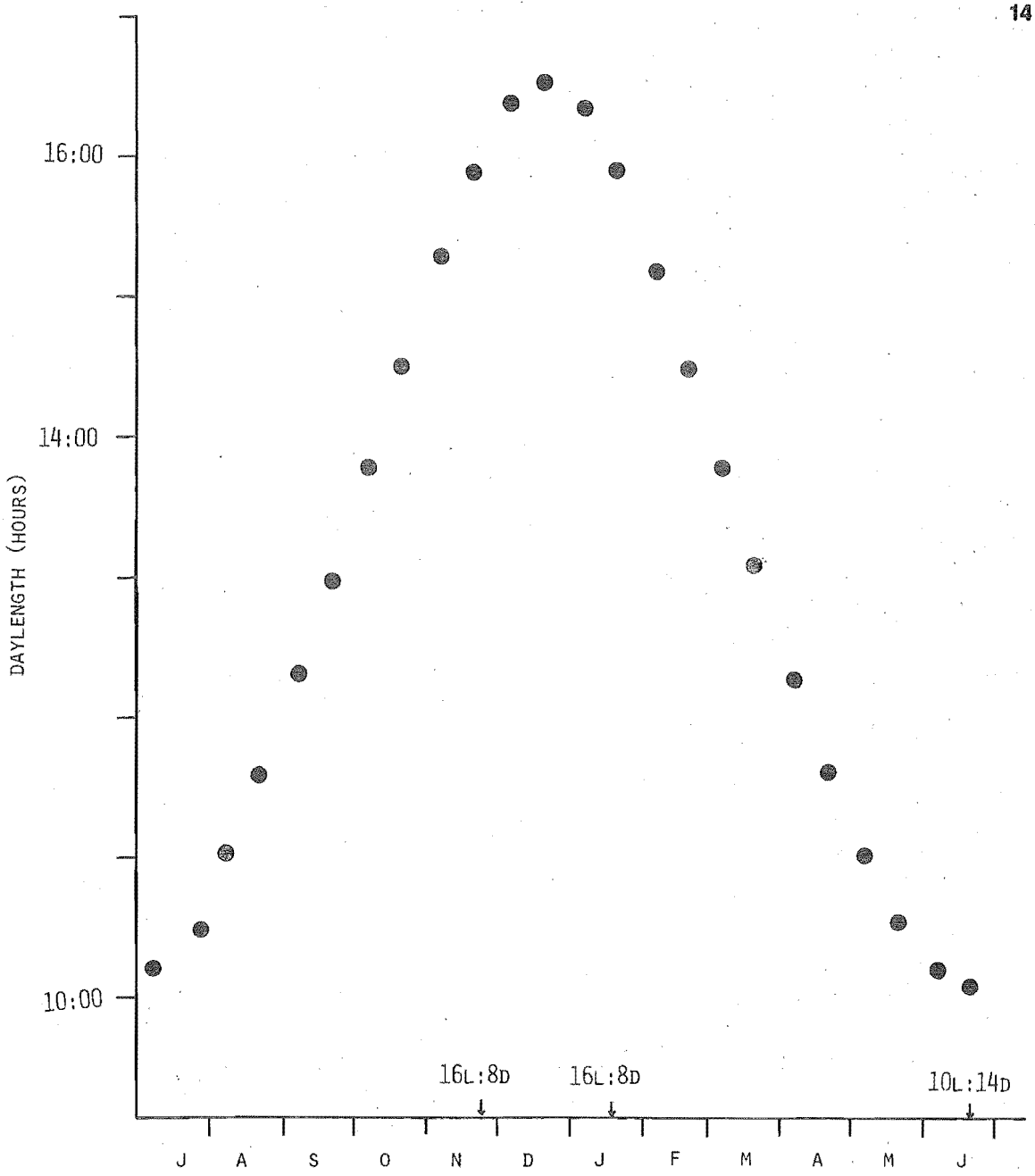
3.3.4. Water Level Fluctuations

Water level fluctuations were measured using a wooden stake, driven into the substrate and marked to show the initial water level. Records were kept of the direction and change in water level at each subsequent visit to the study area.

3.3.4.1. Isaac's Pond A recurring seasonal trend in water level fluctuation was noted. The water level decreased during the summer and then increased to a maximum level during the winter. The cyclic seasonal minimum water level was recorded on 26 April 1976, 8 December 1976 and 1 April 1978. The cyclic seasonal maximum water level was recorded on 13 August 1977 and 2 August 1978. The difference between the maximum and minimum water level was 0.29m in 1976 - 1977 and 0.46m in 1977 - 1978. The annual maximum water level was not recorded during 1975; therefore, the difference in water level could not be calculated for that year. The minimum water level of the three years was recorded on 26 April 1976, and was 0.10m lower than the next lowest level recorded on 1 April 1978.

Overall the aquatic vegetation in the channel was affected only slightly by the water level fluctuations; however, the marginal vegetation occasionally dried out completely as seen during the period February - April 1976 in the area from which I collected exuviae.

Fig. 14. Day length, from the start of Civil Twilight in the morning to the end of Civil Twilight in the evening during 1977 at Lake Sarah, 43°03'S; 171°47'E.


16:00
14:00
10:00
DAYLENGTH (HOURS)
16L:8D
16L:8D
10L:14D
J
A
S
O
N
D
J
F
M
A
M
J

3.3.4.2. Lake Sarah The water level was measured only in Lake Sarah - tb. Seepage between the lake and the *Typha* - bed resulted in virtually the same water level in both areas.

No recurring seasonal trend in water level fluctuation was apparent. During the observations the water level rose from 30 October 1976 to a maximum of 0.09m above the initial water level by 6 March 1977, then fell slowly to a minimum of 0.10m below the initial water level by 26 February 1978, after which the water level began to rise again.

Some shallow areas within Lake Sarah - tb dried up completely and others became anaerobic during the dry period ending 26 February 1978. Lake Sarah - ls was affected only slightly; the water level always reached the base of the marginal vegetation on the shore.

3.4. SUMMARY

The climate at each study site reflected the general features of the particular climatic region in which it was located. Local climatic effects, however, had a profound influence on the sites and combined with various physical features made the sites distinctly different. Major differences were observed in the temperature regimens experienced and to a lesser degree differences were noted in the effects of water level fluctuations on the sites. Photoperiod is almost identical at Isaac's Pond and Lake Sarah and is treated as a constant factor in this study. The difference in the temperature regimen experienced during the years of study at Isaac's Pond and Lake Sarah was large, whereas the difference between the Lake Sarah sites was slight. Water level fluctuations were severe at Lake Sarah - tb only during the dry 1977 - 1978 season when areas within this site dried out completely. They were severe at Isaac's Pond only at irregular intervals when the water level dropped markedly.

Characteristically Isaac's Pond, based on the water temperature regimen, experienced long cool summers and short warm winters. The temperature was moderated both by the local climate, which was influenced mainly by the close proximity of the ocean, and especially by the artesian water source. Rainfall was seasonal at Isaac's Pond with a winter maximum. Large water level fluctuations occurred during the year; however, only extremely low water levels affected the

habitat, for example, the period February to April 1976.

Compared with Isaac's Pond, Lake Sarah - tb experienced shorter summers (because of the local climate) that possibly were warmer (because of the shallow nature of the site). The local climate was influenced mainly by the almost continuous winds, by the altitude, and by the inland location. At Lake Sarah - tb the summer started later and ended earlier, and the winter was longer and cooler than that at Isaac's Pond. No recurring seasonal rainfall pattern was noted, probably because Lake Sarah is located in a rainfall gradient area, but wet years and dry years did occur. The *Typha* - bed was severely affected by even a slight decrease in the water level.

Compared with Lake Sarah - tb, Lake Sarah - ls experienced moderated daily and annual temperatures because of the large volume of water which was almost constantly mixed by the winds. Therefore, Lake Sarah - ls heated and cooled relatively slowly with a lower maximum and higher minimum temperature than the ones recorded in Lake Sarah - tb. Compared with Isaac's Pond, Lake Sarah - ls experienced shorter, slightly cooler summers and longer, cooler winters. The water level fluctuation had no apparent effect on Lake Sarah - ls.

A brief summary of the major year to year differences in the physical conditions and water level fluctuations experienced at each site is necessary to facilitate correlation with field observations later in this work. At Isaac's Pond water temperatures during the summer were similar from year to year. The winter of 1976 was slightly warmer than that of 1977. Cold conditions continued longer during October - November 1976 and warm conditions continued through to April in 1978. The water level reached its lowest level during the period February to April, 1976 and its second lowest level during this period in 1978.

At Lake Sarah - tb water temperatures were similar during January - February of 1977 and 1978. Cold conditions continued longer during November - December 1977 and warm conditions continued through to April in 1978. During the period 1976 - 1977 the water level rose slightly, whereas during the period 1977 - 1978 the water level fell slightly. This same pattern, although moderated, was believed to occur at Lake Sarah - ls as well.

Hodgkin & Watson (1958) noted that odonate larvae in shallow, temporary ponds experienced rapid growth rates at high temperatures. However, they also noted that *Acanthaeshna anacantha* (Tillyard), a species with a one-or two-year life cycle that lives in permanent hill streams, showed little or no acceleration of growth at 21.1°C and retarded growth and high mortality at 29.4°C. This may indicate that species restricted to cool, permanent habitats experience retarded growth and high mortality at high temperatures.

Of the species studied, *X. zealandica* and *A. colensonis* probably belong to the former group (rapid growth at high temperatures) because they are found throughout New Zealand, including small, shallow ponds. *P. smithii* and *P. grayi*, however, may belong to the latter group (retarded growth and high mortality at high temperatures) because they are restricted to relatively cool lakes and streams, primarily in mountain areas. With this in mind an examination of the climatic summaries can provide some insight into the likely growth patterns exhibited by the larvae present at the various sites.

For *X. zealandica* and *A. colensonis* at Isaac's Pond the period suitable for growth is long, but because the summers are not intensely hot (maximum 21°C) there is no period when rapid growth can occur. Because temperatures average about 10°C during the winter, growth may continue at a reduced rate.

At Lake Sarah - tb and Lake Sarah - ls the period suitable for growth is much shorter. Some localised areas within Lake Sarah - tb probably experience temperatures higher than the observed maximum of 23°C; therefore, some rapid growth may be possible for a short period. However, this could not occur in Lake Sarah - ls because of its moderated temperatures. During the winter, temperatures are probably low enough to prevent growth at both Lake Sarah sites.

These different growth patterns must be reflected in the life cycle and/or in the emergence of *X. zealandica* and *A. colensonis* at the various sites. If the above assumptions about the growth patterns are correct then the life cycle of these odonates at Isaac's Pond would be completed in less time, and emergence would begin earlier and perhaps continue longer, than at Lake Sarah.

For *P. smithii* and *P. grayi* a relatively cool, permanent body of water in the mountains, such as Lake Sarah, is a characteristic habitat. The period suitable for growth is short and low temperatures

during the winter probably prevent growth. The life cycles of the two *Procordulia* spp. are possibly longer than those of the two zygopterans and may differ in other respects also. No study of *P. smithii* and *P. grayi* was carried out at Isaac's Pond; therefore, no comparison of their life cycles at different sites was possible.

The effect of water level fluctuations on larval growth patterns is more difficult to assess. Larvae caught in a habitat that is drying out must either complete their development rapidly or move away from the area, if possible; otherwise they may be killed by the ensuing anaerobic conditions or through desiccation. This in turn would prematurely end emergence from the area or perhaps make that area unsuitable for further emergence.

FIELD STUDY

The field study was designed to provide an accurate account of the pattern of seasonality of the species under study. Information on larval growth, dormant stages (quiescence or diapause) and the timing of dormancy was provided by a larval survey. This larval survey followed the pattern of changes in the size - class frequency distribution of the population and thereby provided some insight into the degree of synchronisation exhibited in the various life stages. An adult emergence study provided a more reliable indication of the degree of synchronisation within the life cycle. Seasonality differences observed between the odonate populations, mainly of *X. zealandica*, at Isaac's Pond and Lake Sarah were examined and an attempt was made to correlate the differences observed with the climatic differences noted between the two areas.

4. LARVAL SURVEY

4.1. INTRODUCTION

The chief objects of the larval survey were considered comparable to those described by Elliott (1977) for a faunal survey:

- to discover which species are present; and
- to estimate the relative abundance of each species.

In this study, the larval survey was designed to determine which size - classes of the odonates were present and to estimate the relative abundance of each size - class at the study site at the time of sampling. The faunal survey deals with a multi species group and its species composition, whereas the larval survey deals with single species groups and their size - class composition. The changing pattern of size - class frequency distribution was followed by means of sampling at regular intervals (approximately monthly) during the year.

The larval survey employed the same sampling techniques as those used in a faunal survey. Large samples were taken from the biotopes (*e.g.* stony substratum, mud, plant groups, *etc.*, see Elliott 1977) in the study area to obtain even the less abundant size - classes. The simplest sampling method involved collecting

over a specified area with a pond net. A high proportion of the total size - classes present in the population were caught without need of elaborate equipment. The results obtained by this method are comparable when the biotope and collector are the same (Elliott 1977). Therefore, it was possible to compare the size - class frequency distribution in the population of one sample, with that of another sample from the same biotope, and to compare samples from the same biotope made at various times of the year. The survey, as designed, gave no estimate of numbers per unit area; only the relative abundance of each size - class was important in this study.

4.2. SAMPLING, SORTING AND ANALYSES

4.2.1. Sampling

Samples were taken with a triangular pond net. The leading edge was 0.44m long and the two sides attached to the handle were 0.38m long. The internal mesh size of the netting used was 1.0 by 1.1mm; 1.5mm across the diagonal.

To obtain a sample the pond net was swept over a distance of 1.0m through the aquatic vegetation or debris. This was repeated three times in the same area, to make up one sample. In areas of dense emergent vegetation the corner of the net was forced between the stems of the plants to obtain material.

The samples were placed in plastic bags, each assigned a sample number, and either preserved immediately or returned fresh to the laboratory. Unpreserved samples were sorted as soon as possible, usually within 24 hours. If larvae were required for laboratory experiments samples were stored at 4°C and 16L : 8D for no longer than seven days. Material that had not been sorted by this time was preserved. All samples were preserved in 10% formalin as this was found to be a reliable fixative for the large quantity of material involved in each sample.

Two biotopes were recognised at Isaac's Pond:

- 1. the edge, consisting mainly of submerged roots and emergent stems of *J. gregiflorus* in the shallow water along the margin of the channel; and

- 2. the bottom, consisting mainly of a dense mat of *E. canadensis* and *Spirogyra* sp. in the centre of the channel.

At least one sample was taken from the edge and three samples were taken from the bottom at each visit. The pattern of changes in the size - class frequency distribution of the population was determined from the bottom samples, whereas the samples from the edge were used as a means of monitoring possible deviations from the observed pattern. Sampling was carried out over approximately a two year period, August 1975 to March 1977. Before repeating a sample in any area a recovery period of at least 12 months was allowed.

At Lake Sarah - tb the biotopes were indistinct because of variable water depth and plant species composition; therefore, up to ten samples from various areas were taken during each visit to give an overall view of the pattern of changes in the size - class frequency distribution of the population. Sampling was carried out over approximately a one year period, February 1976 to March 1977. No sample was taken from the same area twice.

4.2.2. Net Check

The effectiveness of the netting in retaining the size - classes of each species was tested in the laboratory using an open-ended cylinder, 140mm in height with an internal diameter of 100mm, made of opaque, smooth plastic. One end of the cylinder was sealed with a screw-cap, fitted with a clear plastic tube, 30mm long with an internal diameter of 10mm. The netting used in taking samples was stretched across the open bottom of the cylinder and held in place by an elastic band. The assembled unit was held vertically in a 200mm column of water kept at 20°C. Live larvae, either reared in the laboratory from the egg or collected in the field, were added to the cylinder through the small plastic tube. The numbers and sizes of the larvae 'actively' crawling through the netting in one hour were recorded and the larvae were returned to the cylinder. Subsequently the cylinder was submersed to the base of the small plastic tube and then lifted out of the water. This was repeated five times in a 30-second period. The numbers and sizes of the larvae 'passively' washed through the netting were recorded and the larvae were returned to the cylinder. The tests were run alternately, starting at about 8:00 and continuing to about 16:00 of the same day. Each test was run

five times. The above procedures were similar to those that Lawton (1970) used to determine the ability of small *Pyrrhosoma nymphula* (Sulzer) larvae to escape through netting.

Larvae were assigned to approximate instars (see section 2.) on the basis of head width and body length measurements to obtain an estimate of the number of moults necessary before all of the larvae were retained by the netting. The results are presented as the mean percentage of larvae passing through the netting in five trials (Tables 5 to 7).

No third instar larvae of *X. zealandica* and no larvae of *P. smithii* beyond the second instar were available for testing. The *X. zealandica* larvae had moulted beyond the third instar when testing was carried out. In *P. smithii* no successful rearing technique was found to obtain the later instars. Of the larvae tested, almost all the second instars passed through the netting passively. About 80% of the zygopterans were retained after reaching a head width of about 0.60mm at approximately the fourth instar. These results indicate that the presence of a new cohort in the field would not be noticed until the larvae had moulted into the fourth or perhaps the third instar. This may also apply to *P. smithii*. The fourth instar larvae of *P. smithii* collected in the field had a head width of approximately 0.60mm.

Jonasson (1955, 1958) showed that chironomid larvae were retained when the width of the chitinous head capsule exceeded the mesh size of the sampler. He found that although the thorax was wider than the head the larvae passed through the netting if the head capsule was smaller than the mesh size. Results for the zygopterans showed that almost all the larvae with a head width of 1.00 to 1.10mm were retained by a mesh size of 1.0 by 1.1mm. Larvae of *X. zealandica* with a head width of 1.32mm were capable of active movement through the net. The larvae probably passed through the net on the diagonal (1.50mm); however, at a head width of 1.63mm all larvae were retained.

Netting with a mesh size of 0.30mm by 0.30mm, which was probably suitable for the retention of all the instars, was tested in the field. Because of clogging of the net by fine silt, algae and debris, samples could not be made effectively and use of this mesh size was discontinued. Lawton (1970) found that a net mesh of less than

TABLE 5. Mean percentage of *Xanthocnemis zealandica* larvae passing through the netting used in sampling.

Mean Head Width (mm)	Approximate Instar	Number per Trial	Percentage of larvae passing through netting in five trials	
			Active (1 h)	Passive (30 sec)
0.33	2	20	26.6	100
	3	None available	-	-
0.76	4	16	15.2	20.0
0.99	5	20	10.5	4.0
1.32	6	32	5.7	0.6
1.63	7	11	0	0

TABLE 6. Mean percentage of *Austrolestes colensonis* larvae passing through the netting used in sampling.

Mean Head Width (mm)	Approximate Instar	Number per Trial	Percentage of larvae passing through netting in five trials	
			Active (1 h)	Passive (30 sec)
0.36	2	44	64.5	93.6
0.47	3	32	36.9	59.4
0.60	4	18	16.7	17.8
1.10	5	14	0	0

TABLE 7. Mean percentage of *Procordulia smithii* larvae passing through the netting used in sampling.

Mean Head Width (mm)	Approximate Instar	Number per Trial	Percentage of larvae passing through netting in five trials	
			Active (1 h)	Passive (30 sec)
0.42	2	20	100	100

1.0mm clogged during sampling; however, he considered a 1.0mm net mesh satisfactory for his studies. During my studies clogging also occurred when the usual sampling net (1.0 x 1.1mm mesh) was used, but never to the extent that the net was blocked completely. This clogging probably increased the effectiveness of the netting in retaining early instars; although no second instar larvae of *X. zealandica* were passively retained by the net in the laboratory they did show up in field samples. Second instar larvae of both *A. colensonis* and *P. smithii* were also recovered from field samples. However, as stated before, the presence of a new cohort in the field would not be clearly recognised until the larvae had reached the fourth or perhaps the third instar.

4.2.3. Sorting

Material to be sorted was first carefully washed in a sieve with a 300mμ mesh size to remove the fine silt. Unpreserved material was then placed in water in a white plastic tray and sorted by hand under a bank of three 40 watt incandescent lamps and one 20 watt fluorescent lamp. The sample was drained and preserved and later resorted using sugar flotation, modified after Anderson (1959) and Hynes & Hynes (1975). Preserved material, after washing and draining, was placed in a clear plastic tank, 0.27m wide by 0.41m long by 0.20m deep, then a sugar solution with a specific gravity of 1.120 was added to a depth of 60 to 70mm. The sample was sorted under the lighting as described above, in the following manner. The material in the sugar solution was stirred thoroughly and any clumps of material were broken up. The vegetation was allowed to sink, then any odonate larvae at the surface were transferred to 10% formalin. The stirring and sorting procedure was continued until three consecutive searches failed to produce larvae. Second instar larvae of the various species were found to float for at least two hours before sinking. The sugar solution was then poured through the sieve and the specific gravity readjusted to 1.120. Sorted material was rinsed with water, drained and stored in 10% formalin for possible future reference.

4.2.4. Sorting Effectiveness

The effectiveness of the sugar flotation technique in the recovery of larvae was checked using two procedures. Firstly, a sample from Isaac's Pond which had previously been sorted using the sugar flotation technique was subsequently sorted by hand using a Wild M5 dissecting microscope at X6 total magnification. The sample was selected for resorting on the basis of the degree of difficulty experienced during the initial sorting using sugar flotation. A high *Spirogyra* content made the initial sort relatively difficult as larvae became entangled in the filaments which prevented the flotation of some individuals. Initially 41 *X. zealandica* larvae and two *A. colensonis* larvae were recovered by sugar flotation. An additional seven *X. zealandica* larvae, all with a head width less than 1.20mm, were recovered during hand sorting. The overall efficiency of recovery using sugar flotation was 86%.

In a second check to determine the effectiveness of the sorting technique 90 larvae representing the size-classes of *X. zealandica* were added to the material which had been hand sorted in the first check as described above. The sample was then washed and sorted using the sugar flotation technique as previously described (section 4.2.3.). A total of 91.1% of the larvae were subsequently recovered. Again, all the larvae that remained unrecovered had a head width of less than 1.20mm.

Gerking (1962) found that his sugar flotation technique was 90 to 99% efficient in recovering invertebrates, excluding molluscs, from bottom samples and Fast (1970) found his sugar flotation technique to be 87% efficient in the recovery of preserved chironomid larvae from samples that contained coarse sand and plant debris. In work using benthic stream samples Pask and Costa (1971) found the efficiency of their sugar flotation technique to vary from 71.5 to 100% recovery depending on the taxa, and that recovery was always higher from preserved samples than from unpreserved samples. The efficiency of 86 to 91% recovery as found in my tests agrees well with the results obtained in the above works and indicates that the sugar flotation technique is perhaps as useful for the sorting of samples high in organic matter as for the sorting of samples containing mainly sand or gravel.

The recovery of larvae was biased in favour of the size - classes with a head width greater than 1.20mm. All larvae with a head width greater than this were probably recovered during sorting. This loss of small larvae during sorting combined with the loss during sampling (section 4.2.2.) indicates the possibility of under-representation of the smaller size - classes within the size - class frequency distribution of the larvae. Above a head width of 1.20mm almost all the individuals in the population are recovered.

4.2.5. Measurements, Metamorphosis and Preservation

Head widths and wing pad lengths were determined as described earlier, in section 2. . All measurements for the larval survey were made to the nearest 0.04mm.

Metamorphosis of final instar larvae taken in larval collections was used to predict the start of emergence. Three stages of metamorphosis, designated early, mid and late, could be easily recognised in the zygopterans. Early metamorphosis was distinguished by swelling of the wing pads and the folding of the anal veins. Mid-metamorphosis was distinguished by the folding of the costal veins in the wing pads. Late metamorphosis, usually followed by emergence within one or two days, was distinguished by black granules appearing in the wing pads. In *P. smithii* no attempt was made to recognise stages of metamorphosis. Larvae with their eyes touching mesially and swollen wing pads were considered to be in metamorphosis.

After examination, all larvae were stored in 70% ethanol plus 1% glycerine, which kept specimens supple even after a lengthy period of storage.

4.2.6. Sampling Effectiveness

4.2.6.1. Accuracy As mentioned previously the larval survey was designed to estimate the relative abundance of each size - class present in the population. The accuracy of this estimate was examined by comparing samples obtained using a quantitative sampling device, with samples obtained in the manner described in section 4.2.1.. The size - class frequency distribution of *X. zealandica* larvae was determined for each sample and the results were compared to establish if the size - class frequency distributions were similar in paired

samples. If the size - class frequency distributions were the same then the estimate made using the pond net could be considered reliable even though of a qualitative nature.

All attempts to take quantitative samples at Isaac's Pond met with failure because of the nature of the area sampled. The dense mat of *E. canadensis* and the stony bottom, combined with the relatively deep water, made quantitative sampling extremely difficult without the construction of special equipment. Instead, samples were taken at Shipley's Large Pond (section 3.3.1.1.). This pond also had a dense mat of *E. canadensis* and a stony bottom, but because the water was shallower than at Isaac's Pond it was considerably easier to take quantitative samples.

Quantitative samples were taken with a cylinder fitted with a ring of teeth at one end and handles at the top. The operation of this device was similar in concept to the 'drop box' used by Benke & Benke (1975). When driven into the substrate the teeth at one end of the cylinder severed the vegetation and enclosed an area of $0.05m^2$. The sampling method was modelled after that described by Hynes (1971) for retrieving fauna from box or cylindrical samplers used for quantitative sampling in flowing waters. All coarse materials were removed by hand and preserved in 10% formalin. The remaining material was stirred thoroughly and the bottom dug up. A small dip net with internal mesh size 0.30mm by 0.30mm and 0.40mm across the diagonal was used to stir the water and to catch the remaining animals. Stirring was repeated until three successive attempts failed to catch any animals.

A qualitative sample, using the pond net, was taken adjacent to the cylinder while it was still in position, before its contents had been removed and the surrounding area disturbed.

Comparative samples were taken at two locations in Shipley's Large Pond on 25 November 1975. All samples were preserved and returned to the laboratory for sorting. The head width size - class frequency distributions were tested for homogeneity using a Mann-Whitney U test for large samples (Siegel 1956).

At the first location the quantitative sample size (n_1) was 48, the qualitative sample size (n_2) was 144, the calculated U statistic was 3277.5 and Z statistic was 0.54 from which the probability for a two tailed test was 0.5892 (not significant). At the second location

the quantitative sample size (n_1) was 41, the qualitative sample size (n_2) was 174, the calculated U statistic was 3369.5 and Z statistic was 0.55 from which the probability for a two tailed test was 0.5824 (not significant). The null hypothesis that the paired quantitative and qualitative samples were drawn from the same population and, therefore, had the same size - class distribution was accepted.

Although these results indicate the quantitative and qualitative collection techniques to be comparable previous results, as seen in section 4.2.2., show that larvae with a head width smaller than about 1.00 to 1.10mm can pass through the pond net during sampling. By 25 November 1975 only about 9% of the larvae in the quantitative and 6% of the larvae in the qualitative samples taken at Shipley's Large Pond had a head width of less than 1.10mm. Because of the size - class frequency distribution of the larvae at this time the pond net was actually suited to collect almost all of the population present. Therefore, the difference between the size - class frequency distribution of the larvae collected by the quantitative and the qualitative samplers are slight at this time. At other times of the year, when a larger proportion of smaller larvae is present in the population, the differences in results between the two sampling techniques could be more pronounced. The results obtained in these tests, on 25 November, do show conclusively that the pond net provides an accurate estimate of the size - classes present when the head width of the larvae is greater than 1.10mm.

4.2.6.2. Reliability As indicated in section 4.2.1. three samples were taken from the bottom biotope at Isaac's Pond during each visit. The head width size - class frequency distributions of the *X. zealandica* larvae from these samples were determined. Periodically the samples were compared using the Mann-Whitney U test, as described in section 4.2.6.1., to establish if the size - class frequency distribution of the population varied significantly within the biotope. The results (Table 8) all show that samples taken on the same day in the same biotope do not differ significantly in the size - class distributions obtained. Pooling the results of the monthly samples was justified because the samples were apparently

taken from the same population of larvae. The larvae appeared to be evenly distributed at Isaac's Pond probably because of the uniform nature of the channel biotope.

TABLE 8. The probability that samples collected on the same date at Isaac's Pond were drawn from populations having the same head width size - class distribution. Analyses made using the Mann - Whitney U test for large samples (Siegel 1956).

Collection Date	Sample Size n_1	Sample Size n_2	U	Z	Probability for a Two Tailed Test
20 September 1975	39	40	669.0	1.0884	0.2758 Not significant
25 February 1976	163	220	16203.0	1.6128	0.1074 Not significant
28 October 1976	26	36	405.0	0.8987	0.3682 Not significant
23 March 1977	20	80	2181.5	0.9200	0.3576 Not significant

At Lake Sarah - tb the size - class frequency distribution especially, and even the numbers of each species of larvae found, varied considerably from sample to sample probably because this site is made up of a large number of biotopes. Therefore, an overall, composite size - class distribution for the entire population was obtained by sampling from as many areas as possible and pooling the results. Because of the variable nature of the samples these pooled results are less reliable than those obtained at Isaac's Pond. The size - class frequency distribution estimates were assumed to be valid because they were based on a sampling program that was kept constant and relatively large numbers of samples were taken from several areas on each collection date.

4.2.7. Analyses of Size - Class Frequency Distribution

The pattern of development of the larval population at the study areas was determined by following the pattern of change in the head width size - class frequency distribution from month to month. The monthly size - class frequency distribution of each species was calculated from 50 or more larvae when possible. These were obtained

by sorting an appropriate number of samples to provide a combined total of at least 50 larvae. On only a few occasions were less than 50 larvae obtained by combining samples. The results are presented graphically, first as kite diagrams and then as the component cohorts.

The kite diagrams present the percent frequency of each size - class, showing the overall distribution within the population. For the kite diagrams the head width size - classes were combined to form 0.08mm clas intervals and 0.20mm class intervals for the zygopterans and *P. smithii*, respectively.

The head width size - class frequency distributions for each month were separated into component cohorts. A computer program for Taylor's method for polymodal analysis (Taylor 1965) (developed by K.W. Duncan and D. Chang, Zoology Department, University of Canterbury, Christchurch) was used for this when necessary. The mean head width and one standard deviation was then calculated for each cohort and a growth curve was produced for the various species by plotting and joining the monthly values.

Each cohort was assigned a number at the left side of the graphs or at the position on the graphs at the point where the cohort first appeared. Arrows were used in the kite diagrams to indicate the region of separation or overlap between cohorts.

4.3. *XANTHOCNEMIS ZEALANDICA*

4.3.1. Isaac's Pond

4.3.1.1. Results From Fig. 15, small larvae first appeared during February 1976 (cohort 3) and January 1977 (cohort 4). The mean head width of cohort 3 (Fig. 16) had increased markedly by March 1976 after which the rate of increase was slow until September. The mean head width increased more rapidly from September to March 1977 by which time cohort 3 had attained a mean head width of 2.33mm, a size similar to that attained by cohort 2 (2.11mm) by March 1976.

In cohort 2 the mean head width increased at a slow rate from April until September 1976, then increased more rapidly until the last of the cohort disappeared during February 1977. Cohort 1 showed a similar pattern during 1975-1976, with a rapid increase in size from November until the cohort disappeared during February.

The size of the F and F-1 instars decreased during the warmer months (Fig. 15). This was particularly noticeable in cohort 1

Fig. 15. Kite diagram showing head width size - class frequency distributions of *Xanthocnemis zealandica* larvae at Isaac's Pond. Sample size on each collection date indicated at top of graph. Arrows indicate the region of separation or overlap between cohorts.

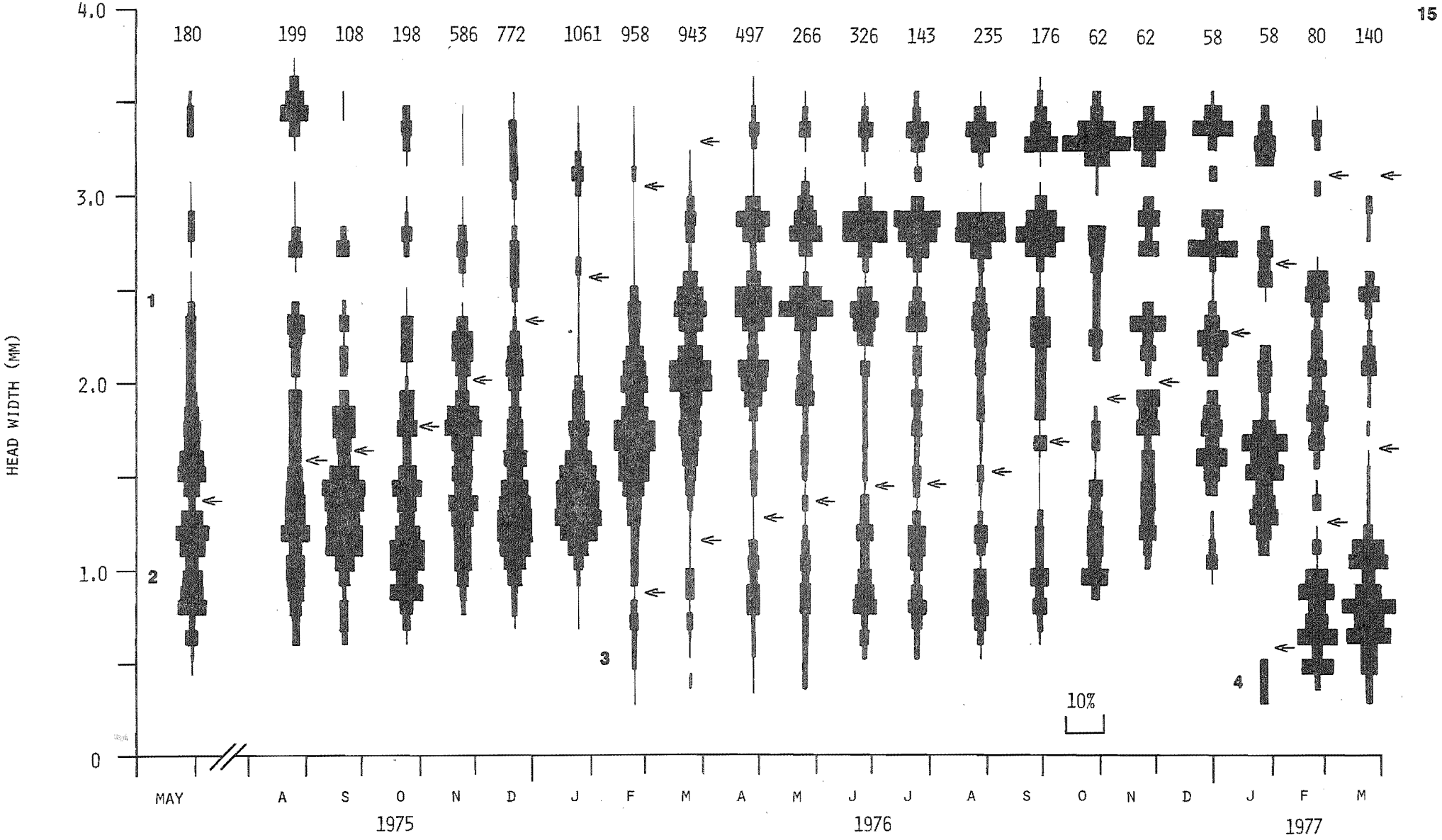
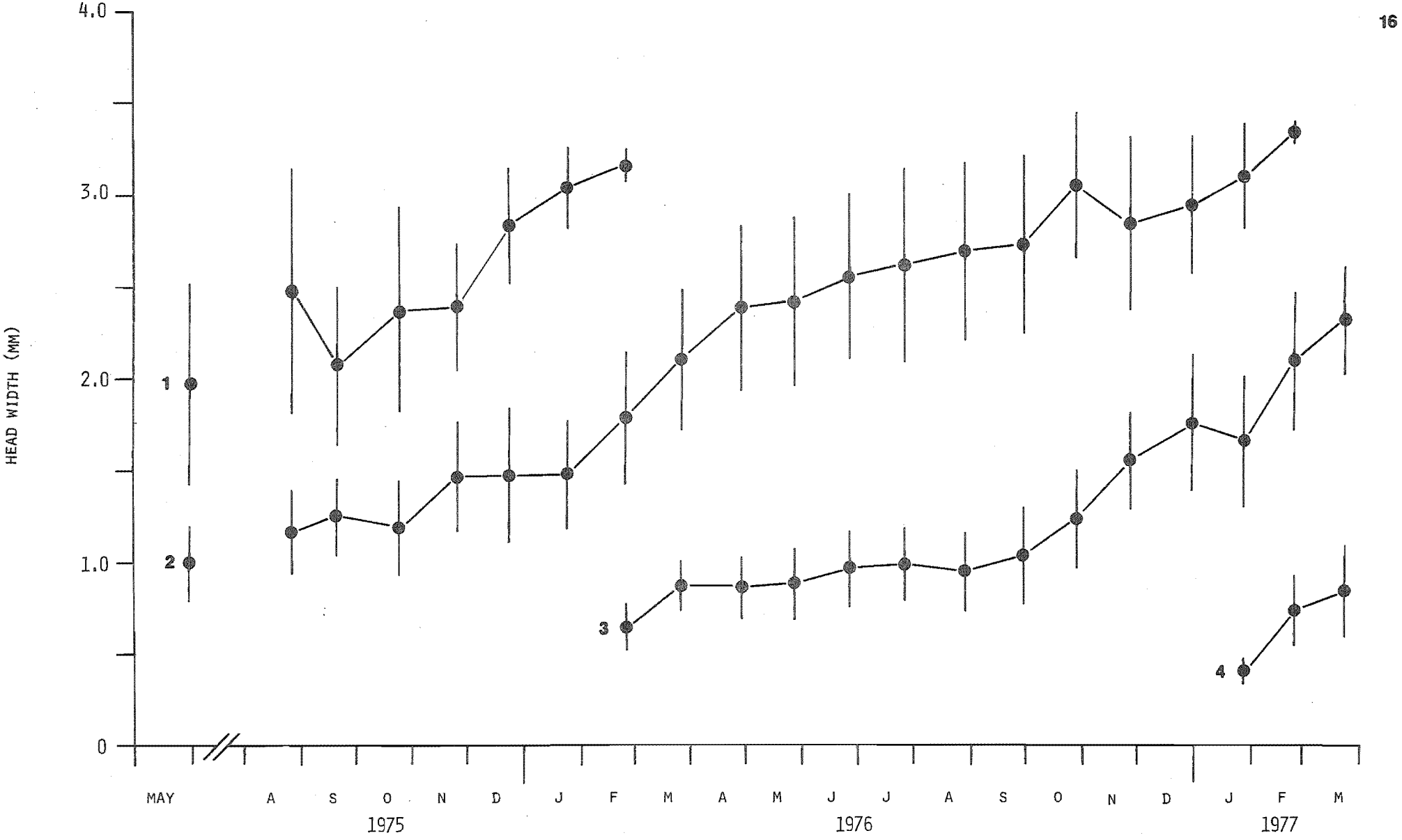

4.0
3.0
2.0
1.0
0
HEAD WIDTH (MM)
180
199
108
198
586
772
1061
958
943
497
266
326
143
235
176
62
62
58
58
80
140
1
2
3
4
10%
MAY
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
1975
1976
1977

Fig. 16. Component cohorts of *Xanthocnemis zealandica* larvae in the population at Isaac's Pond. (Mean ± one standard deviation shown).


4.0
3.0
2.0
1.0
0
HEAD WIDTH (MM)
1
2
3
4
MAY
A S O N D J F M A M J J A S O N D J F M
1975
1976
1977

during the period from August 1975 to February 1976 (Fig. 15). For example, in cohort 1 the mean and standard deviation of the head width of the F instar was 3.39 ± 0.08mm in August (n = 32), 3.34 ± 0.06mm in October (n = 11), 3.24 ± 0.12mm in December (n = 35), and 3.16 ± 0.10mm in February (n = 20).

In cohort 2 (Fig. 15) during 1975-1976, the maximum size increased at a regular rate until the moult into the F-1 instar during February 1976. The F instar did not appear until April. This sequence was repeated in cohort 3 during 1976-1977. The F-1 instar appeared in February (Fig. 15), but the F instar did not appear until late April, as established by a careful search made at Isaac's Pond after regular collections were terminated. During the period January to April 1978 a careful search for late instar larvae in cohort 4 was carried out at fortnightly intervals. The F-1 instar appeared between early February and mid-February and the first F instar appeared by early April.

4.3.1.2. Comments The appearance of small larvae (Fig. 15) during February 1976 and January 1977 was the first indication of the hatch of cohorts 3 and 4 respectively. The first hatch in cohort 3 probably occurred earlier than 25 February, the date of sampling. At that time larvae in cohort 3 ranged in head width from 0.36 to 0.88mm, whereas in cohort 4, 27 January 1977, larvae were relatively smaller, ranging in size from 0.36 to 0.48mm only. As mentioned earlier (sections 4.2.2. and 4.2.4.) larvae with a head width less than 1.00 to 1.20mm were under-represented in the monthly samples. Because of this both cohorts may have hatched earlier than was indicated by larval samples.

Small larvae (head width 0.36 to 0.44mm) were present in cohort 3 during 1976 (Fig. 15) until May. Larvae of this size were not collected again until January 1977 which indicated the first appearance of cohort 4. The disappearance in May of small larvae from cohort 3 was interpreted as the end of the hatching period in the field.

From Fig. 16 in both cohort 3 and 4 the mean head width was approximately the same by March, 0.87mm and 0.85mm respectively. Cohort 3 continued to grow, although at a reduced rate, even after the onset of cold weather (April-May) during 1976 (see Fig. 12). The mean monthly water temperature remained about 10 to 11°C from June to September but by September the mean head width of cohort 3 had

increased to 1.04mm. The growth rate increased with rising water temperatures during September and continued at a regular rate until March. By March 1977 the mean size of cohort 3 was 2.33mm.

Cohort 2 (Fig. 16) showed a marked size increase between October and November 1975 but then remained at a mean head width of 1.47 to 1.48mm to January 1976. During the corresponding period in 1976-1977 rapid growth took place in cohort 3. Fig. 15 shows that growth in cohort 2 continued during this period, as indicated by the regular appearance of larger larvae each month. However, it also appeared that a regular recruitment of small larvae occurred (Fig. 15) from a population of larvae with a head width of less than 1.00mm, which was under-represented in the samples. Therefore, the mean head width of cohort 2 remained nearly constant from September to November, until most of the larvae had attained a head width of 1.00mm (Fig. 15, cohort 2 November 1976).

From January to April 1976 the mean head width increased markedly (Fig. 16), but with the onset of cold weather during April - May 1976 (see Fig. 12) a slightly reduced rate of growth was evident. By August 1976, cohort 2 was made up of F to F-5 instars. The percentage composition of each instar in the cohort was: 21.2% in F; 44.6% in F-1; 20.1% in F-2; and 13.1% in F-3 to F-5. Some F instar larvae were found undergoing metamorphosis at this time. Growth continued until February 1977 (Fig. 16) when cohort 2 disappeared from the population.

Cohort 1, by August 1975, was made up of F to F-5 instars. The percentage composition of each instar in the cohort was: 30.2% in F; 12.3% in F-1; 19.8% in F-2; and 37.7% in F-3 to F-5. Some F instar larvae were found undergoing metamorphosis at this time, as was observed in cohort 2 during August 1976. In cohort 1 the relatively high percentage of F instar larvae in the August collection gave rise to a high value of the mean head width for that month (Fig. 16). By September, after the start of emergence (section 5.3.2.), the F instar composed only 3.2% of the cohort which resulted in a noticeable dip in the growth curve. Growth then continued at a fairly regular rate until February 1976 when cohort 1 disappeared from the population.

A decrease in the size of larvae and adults between an early emerging group and a later emerging group; or even within the emergence period of a group, is a commonly recognised phenomenon in the Ephemeroptera and Plecoptera (see for example, Macan 1957; Elliott 1967; Coleman & Hynes 1970; Benech 1972; and Clifford & Boerger 1974). A similar decrease in the size of larvae has been reported in the zygopterans *Enallagma aspersum* (Hagen) and *Enallagma hageni* (Walsh) (Ingram & Jenner 1976a, 1976b) and in adults of nine of ten species of Platycnemididae and Coenagrionidae examined by Naraoka (1976). In the Anisoptera, Penn (1951) found that the adults of *Pachydiplax longipennis* (Burmeister) that emerged during the first half of the flying season (March through June) were considerably larger than those that emerged during the last half (July through October).

Various authors have suggested this size decrease to be related to food, temperature, substrate, season, stress, or extra moults. Recently Sweeney & Vannote (1978) proposed two hypotheses relating size variation in hemimetabolous insects to temperature. Most of these theories; however, are largely speculative.

The decrease in size of the F instar larvae and exuviae and F-1 instar larvae of *X. zealandica* (Fig. 15) is presented here only as an additional record of this phenomenon in the Odonata. With the information available it is not yet justifiable to relate the size decrease to environmental factors.

The delayed appearance of the F instar in cohort 2, April 1976, and in cohort 3, April 1977 (Fig. 15), and in cohort 4, April 1978, was interpreted as an indication of a growth restriction in the F-1 and/or earlier instars. Prey was abundant during the period from February to April, as large numbers of small arthropods were present in the monthly larval collections; therefore, lack of food did not restrict larval growth. Water temperatures were still relatively high (see Fig. 12); indicating that temperature was not the restricting factor. Because of the above, the growth restriction was probably some form of physiological dormancy. Further details about this dormancy are presented and discussed in later sections (4.3.2.2. and 5.3.2.2.).

4.3.1.3. Summary At Isaac's Pond *X. zealandica* has a two-year life cycle; however, it is possible that a few larvae complete development in one year. The general pattern of development is as follows. The eggs hatch the summer that they are laid. The first winter is spent as early instar larvae with a maximum head width of about 1.28 to 1.56mm. By February of the following summer some larvae are in the F-1 instar but none of these moult into the F instar until April. The second winter is spent as F to approximately F-5 instar larvae. This group completes emergence by the end of the third summer. Some growth occurred during the winter at mean water temperatures of 10 to 11°C. The major period of growth extended from about September to March-April with a possible growth restriction in the F-1 and/or earlier instar larvae during the period from February to April.

4.3.2. Lake Sarah - tb

4.3.2.1. Results From Fig. 17, small larvae first appeared during March 1976 (cohort 3) and January 1977 (cohort 4). The mean head width of cohort 3 (Fig. 18) increased slightly before the next sample was taken in June, but little further growth occurred until September. The mean head width then increased slightly during October and November and markedly by mid-December, after which it increased slowly until March 1977. The mean head width was then 1.33mm, compared with 1.56mm for cohort 2 in March 1976.

The mean head width of cohort 2 apparently decreased by the June sample (Fig. 18), but then little change occurred between June and August. From August the head width increased slowly until October and then at a high, uniform rate until March 1977. The mean head width was then 2.70mm, compared to 2.33mm for cohort 1 in March 1976.

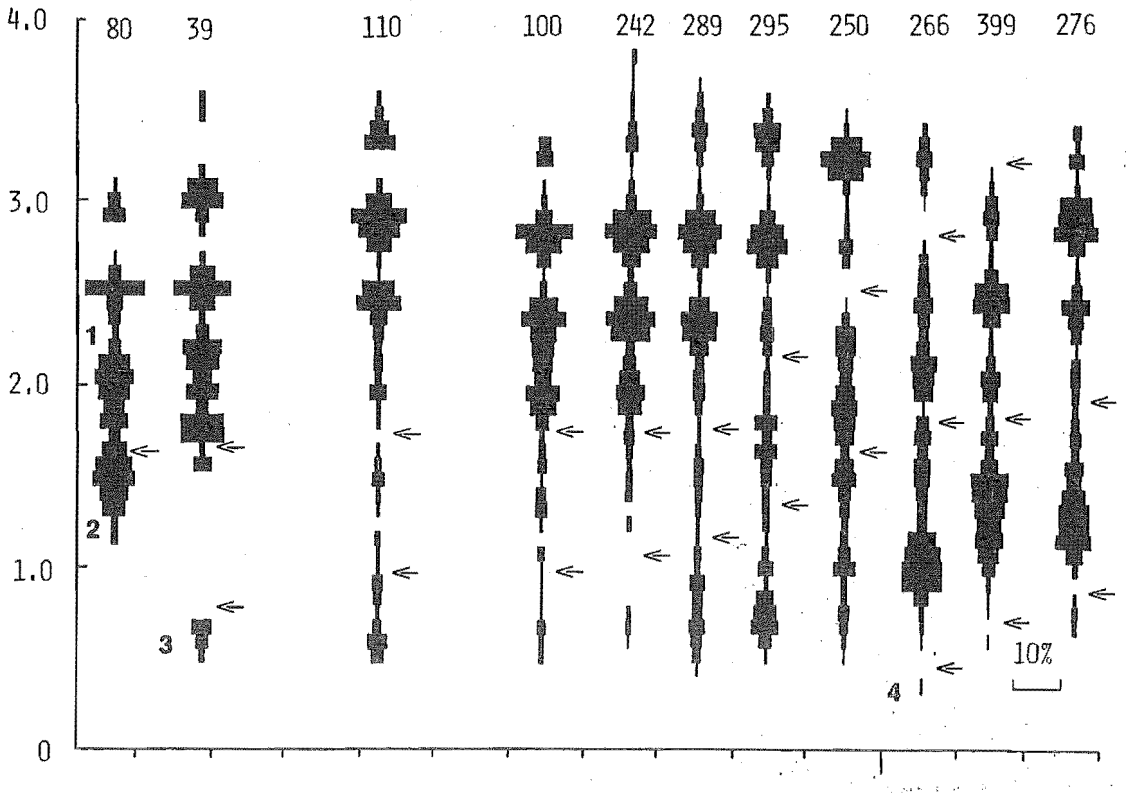
In cohort 1 the mean head width apparently increased by the June sample but in August the mean head width was similar to that observed in March. From August the mean head width increased at a relatively constant rate until the last of the cohort disappeared during January 1977.

The size of the F and F-1 instars decreased during the warmer months (Fig. 17). This was particularly noticeable for the F-1 instar in December 1976 and for the F instar in January 1977. For example, in cohort 1 the mean and standard deviation of the head width of the F instar was 3.41 ± 0.15mm in September (n = 21), it decreased

Fig. 17. Kite diagram showing head width size - class frequency distributions of *Xanthocnemis zealandica* larvae at Lake Sarah - tb. Sample size on each collection date indicated at top of graph. Arrows indicate the region of separation or overlap between cohorts.

Fig. 18. Component cohorts of *Xanthocnemis zealandica* larvae in the population at Lake Sarah - tb. (Mean ± one standard deviation shown).

17


4.0
3.0
2.0
1.0
0
80
39
110
100
242
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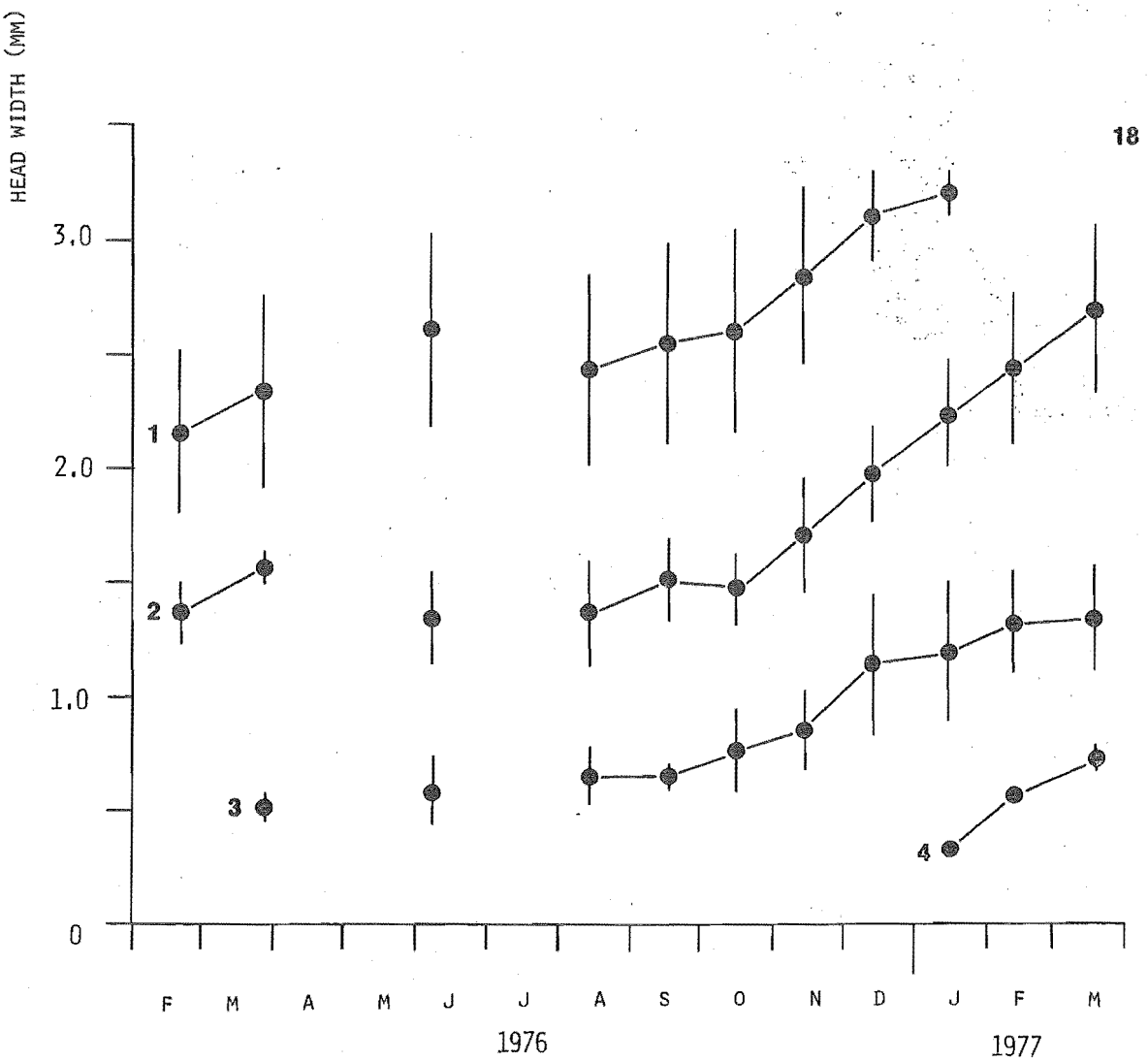
295
250
266
399
276
1
2
3
4
10%

18


HEAD WIDTH (MM)
3.0
2.0
1.0
0
1
2
3
4
F
M
A
M
J
J
A
S
O
N
D
J
F
M
1976
1977

to 3.31 ± 0.10mm by November (n = 51) and reached 3.20 ± 0.10mm by January (n = 27).

In both cohort 1 and cohort 2 (Fig. 17) the F-1 instar was present in February and the F instar first appeared in March. Considerable overlap occurred between cohorts 1 and 2 until November-December after which the cohorts were easily distinguished.

4.3.2.2. Comments The first two samples taken, February and March 1976, appeared unusual when compared with the subsequent collections. Almost no larvae with a head width of less than 1.20mm were collected. Therefore, cohort 3 and possibly cohort 2, which were composed mainly of small larvae at that time, were under-represented in the results. This may have been caused either by a subsequent improvement in sampling techniques; or by movement of the smaller larvae into an inaccessible area, perhaps deep into the bottom debris. Also, the small size of the samples (n = 80 and n = 39) would contribute to the error as would net mesh (section 4.2.2.) and sorting factors (section 4.2.4.). Therefore, the results for cohorts 2 and 3 from February and March 1976 must be treated with caution; although those for cohort 1, which was made up of larger larvae, may be reliable.

The appearance of small larvae (Fig. 17) during March 1976 and January 1977 was the first indication of the hatch of cohorts 3 and 4, respectively. The first hatch of cohort 3 probably occurred earlier than 27 March for the reasons presented above.

Small larvae (head width 0.36 to 0.44mm) were present in cohort 3 from March to August and again in October (Fig. 17). Larvae that hatched the summer that eggs were laid spent the winter as early instars. The absence of small larvae in the September sample but their reappearance in the October sample indicated either a delayed egg hatch, or alternatively a persistence of early instar larvae that was not consistently collected by the sampling technique. Results for *X. zealandica* at Isaac's Pond (section 4.3.1.) indicated that the eggs developed directly, and that the recruitment of small larvae from the size - classes less than 1.00mm continued long after the completion of hatching. This probably applied to the *X. zealandica* population at Lake Sarah - tb as well. This influx of small larvae depressed the growth curve for cohort 3 (Fig. 18) from September 1976 to March 1977 by which time most of the larvae in the

cohort were larger than 1.00mm (Fig. 17).

The mean head width of cohort 3 in March 1977 was noticeably smaller than that of cohort 2 during the corresponding period in 1976 (Fig. 18). As mentioned earlier the small instar larvae in cohort 2 were under-represented in the February-March samples in 1976; therefore, the mean head width calculated was higher than expected. In June the mean head width was 1.34mm which was similar to that of cohort 3 in March 1977 (1.33mm).

In cohort 2 (Fig. 18) no growth took place between June and August. An increase in the mean head width occurred by September-October and growth continued at a uniform rate until March when the mean head width of cohort 2 was noticeably larger than that of cohort 1 for the corresponding period in 1976. Cohort 1 attained a similar size by October-November 1976 (Fig. 18), only after an additional period of growth during the spring. The difference between the mean head width of the cohorts at the end of summer (March) may have represented a difference in growth seasons experienced by the two cohorts.

The mean head width of cohort 1 in June appeared to be unusually high in relation to the similar values obtained for the March and August collections. The results obtained from the June sample may have been related to sampling error. The similarity of the mean head width between March (2.33mm) and August (2.43mm) indicated little growth during that period. Growth started again after August and by October, at the start of emergence (section 5.3.2.), cohort 1 was made up of F to F-3 instar larvae. The percentage composition of each instar in the cohort was: 13.9% in F; 40.4% in F-1; 35.1% in F-2; and 10.6% in F-3. One F instar larva was found undergoing metamorphosis at this time. Growth in cohort 1 continued at a regular rate from October until the cohort disappeared from the population in January. At Isaac's Pond the cohorts completing emergence were present until February (section 4.3.1.2.).

The decrease in the size of the F instar larvae and exuviae and F-1 instar larvae of *X. zealandica* during the warmer months at Lake Sarah - tb is similar to that observed at Isaac's Pond. This recurring pattern indicates that this phenomenon is not limited to one population, and that a seasonal decrease in size is probably a common

feature of this species.

Apparently no delay of moulting into the F instar occurred at Lake Sarah - tb (Fig. 17). The F-1 instar appeared during February and the F instar appeared the following month, whereas at Isaac's Pond the F-1 instar appeared during February and the F instar appeared during April (Fig. 15). Although no growth restriction was apparent in the F-1 instar larvae at Lake Sarah - tb a possible growth restriction was noted in the F instar larvae. Larvae moulting into the F instar in March failed to complete development to emergence even when conditions remained unseasonably warm, as during March and April 1978 (Fig. 13). For further details see section 5.3.2.2. .

A possible growth restriction was also noted in the F-3 and/or the F-2 instar larvae at Lake Sarah - tb. The overlap that occurred between cohorts 1 and 2 up to November (Fig. 17) was eliminated by December, possibly because of delayed moulting in the F-3 and/or the F-2 instars at that time.

The dormancy period suggested earlier (section 4.3.1.2.) probably occurs in the F-3 to the F instars and is manifested by a delay in the development of the larvae. The instar in which dormancy occurs appears to be related to environmental cues and differs from site to site. The nature of the dormancy period in *X. zealandica* is examined in depth in a later section (7.3.4.).

4.3.2.3. Summary At Lake Sarah - tb *X. zealandica* has a three-year life cycle; however, it is likely that a few larvae complete development in two years. The general pattern of development is as follows. The eggs hatch the summer that they are laid, although the onset of cold weather may delay the completion of hatching until the following summer. The first winter is spent as early instar larvae with a maximum head width of about 0.84mm. By March of the following summer some larvae moulted into approximately the F-4 instar. This group spends the second winter as larvae with a head width of 0.96 to 1.88mm. By February of the following year some larvae are in the F-1 instar and the first F instar larvae appear by March. The third winter is spent as F to approximately F-3 instar larvae. This group completes emergence by the end of the fourth summer. No growth occurred during the winter at mean water temperatures of 3 to 4°C. The major period of growth extended from September-October to March-April with a possible growth restriction in F-3 and F-2 instar larvae during the period from

November to December and in the F instar larvae during the period from March to April.

4.4. *AUSTROLESTES COLENSONIS*

4.4.1. Lake Sarah - tb

4.4.1.1. Results From Fig. 19, small larvae first appeared during March 1976 (cohort 2) and March 1977 (cohort 3). The mean head width of cohort 2 (Fig. 20) increased markedly before the next sample was taken in June, but little further growth occurred until August. A considerable increase in the mean head width was evident by September, after which the values decreased at a uniform rate until November. The mean head width then increased at a rapid rate until March 1977 when it was 2.79mm, compared with 2.81mm for cohort 1 in March 1976.

In cohort 1 the mean head width had increased markedly by the June sample, and then little growth took place between June and August. From August the mean head width increased at a uniform rate until December 1976, after which it remained relatively constant until the last of the cohort disappeared during February 1977.

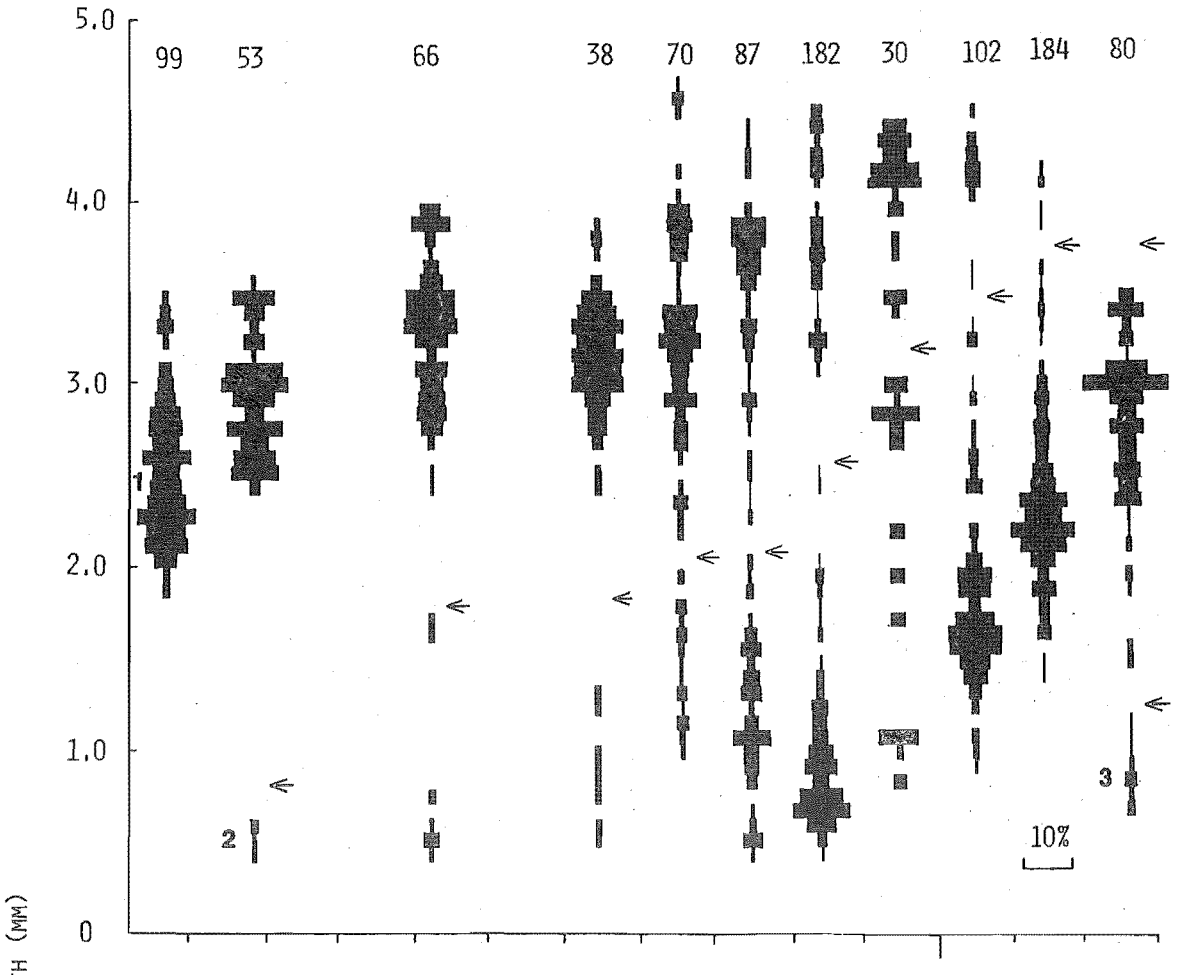
The size of the F and F-1 instars decreased during the warmer months (Fig. 19). This is particularly noticeable for the F-1 instar in January 1977 and for the F instar in February 1976. For example, in cohort 1 the mean and standard deviation of the head width of the F instar was 4.45 ± 0.2mm in September (n = 4), it decreased to 4.29 ± 0.13mm in November (n = 24), and reached 4.03 ± 0.12mm by February (n = 6).

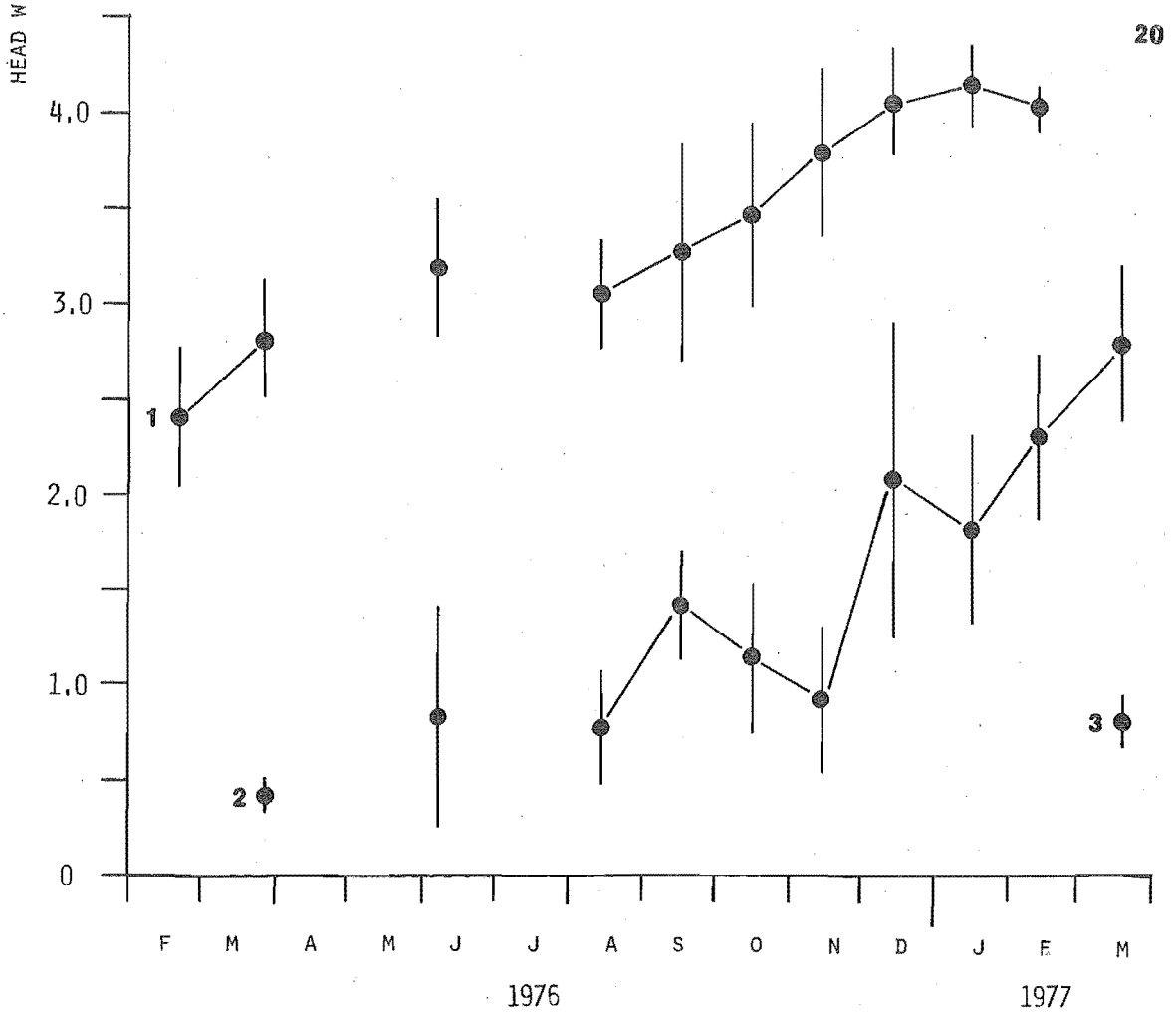
In cohort 1, F-1 instar larvae first appeared between March and June and F instar larvae first appeared in September 1976 (Fig. 19). In cohort 2, F-2 instar larvae first appeared by mid-January 1977 but a careful search at Lake Sarah - tb showed that F-1 instar larvae had not appeared by 20 March but were present by 27 April and that F instar larvae appeared by 1 June 1977.

4.4.1.2. Comments The appearance of small larvae (Fig. 19) during March 1976 and March 1977 was the first indication of the hatch of cohorts 2 and 3, respectively. The larger size of larvae in cohort 3

Fig. 19. Kite diagram showing head width size - class frequency distributions of *Austrolestes colensonis* larvae at Lake Sarah - tb. Sample size on each collection date indicated at top of graph. Arrows indicate the region of separation or overlap between cohorts.

Fig. 20. Component cohorts of *Austrolestes colensonis* larvae in the population at Lake Sarah - tb. (Mean ± one standard deviation shown).


5.0
4.0
3.0
2.0
1.0
0
99
53
66
38
70
87
182
30
102
184
80
1
2
3
10%


HEAD WIDTH (MM)
4.0
3.0
2.0
1.0
0
1
2
3
F
M
A
M
J
J
A
S
O
N
D
J
F
M
1976
1977

in March 1977, as compared with cohort 2 in March 1976 probably means that hatching occurred earlier in 1977 than was indicated by the larval samples (see section 4.3.1.2. p.44).

Apparently no growth occurred in cohort 2 between June and August (Fig. 20). Small larvae with a head width of 0.36 to 0.48mm were present in the June and August samples but were absent from the September sample. The size - class frequency distribution for September (Fig. 19) may be the result of larval growth between August and September; or early instar larvae may have been killed by cold conditions (see Fig. 13); or early instar larvae may have moved preferentially to an area that was not sampled at that time. However, early instar larvae with a head width of 0.44 to 0.60mm reappeared in the cohort during October (Fig. 19) which was believed to indicate the start of a spring hatching period. This conclusion was supported by the increasing number of early instar larvae found in the November sample but not elsewhere. Recruitment of small larvae ended by November (Fig. 19). This is believed to mark the end of the hatching period of cohort 2 in the field. Hatching during the previous season was probably stopped by the onset of cold weather in March-April (see Fig. 13); or alternatively by the intervention of a dormancy period in the egg. The rising temperatures during September-October appeared to stimulate the completion of hatching of cohort 2 at that time.

The influx of small larvae would explain the observed reduction of the mean head width in October and November (Fig. 20). Small larvae were not collected again until the start of the hatching period of cohort 3 in March 1977.

The mean head width for December appeared to be unusually high in relation to the November and January values (Fig. 20). This was probably related to the small sample size for that month (n = 30) of which 14 larvae were in cohort 2. Growth of cohort 2 continued at a regular rate from January to March 1977 by which time the mean head width was similar to that attained by cohort 1 by March 1976.

Cohort 1 grew slightly between the March and June collections 1976 (Fig. 20), and as noted in cohort 2, apparently no growth occurred between June and August, the coldest months of the year (Fig. 13). After August the mean head width increased at a regular rate (Fig. 20).

By October 1976 at the start of emergence (section 5.4.2.), cohort 1 was made up of F to approximately F-4 instar larvae. The percentage composition of each instar in the cohort was: 6.5% in F; 56.5% in F-1; 17.4% in F-2; and 19.6% in F-3 and F-4. None of the F instar larvae in the sample were found to be undergoing metamorphosis at this time. By January 1977 most of the larvae were in the F instar and by February all of the larvae remaining in the cohort were in the F instar.

The slight dip in the growth curve in February (Fig. 20) indicated a decrease in the size of the F instar. As was also observed in *X. zealandica* (sections 4.3.1.2. and 4.3.2.2.), *A. colensonis* showed a decrease in size of the F instar larvae and exuviae and F-1 instar larvae during the warmer months. This decrease in size of *A. colensonis* is noted here as an additional record of this phenomenon in the Odonata.

The delayed appearance of the F-1 instar in cohort 2 during January to April 1977 was interpreted as an indication of a growth restriction in the F-2 and/or earlier instars. As in the situation of *X. zealandica* (section 4.3.1.2. and 4.3.2.2.) neither food nor water temperature were limiting growth. Further details about this growth restriction are presented and discussed later (sections 5.4.2.2. and 7.4.3.). Moulting into the F instar is probably related to temperature as indicated by the presence of F instar larvae in the population either before or after winter (see cohort 2, 1977 and cohort 1, 1976, respectively, Fig. 19). After the appearance of the F-1 instar moulting into the F instar apparently takes place if the weather remains warm.

4.4.1.3. Summary At Lake Sarah - tb *A. colensonis* has a two-year life cycle. The general pattern of development is as follows. The eggs begin to hatch the summer that they are laid but, because of the onset of cold weather or possibly a dormancy period, hatching is not completed until the following spring. The first winter is spent as eggs and early instar larvae with a maximum head width of about 1.60mm. By January of the following summer some larvae are in the F-2 instar but larvae do not moult into the F-1 instar until April. The second winter is spent as F or F-1 to approximately F-4 instar larvae. This group completes emergence by the end of the third summer. No growth occurred during the winter at mean water temperatures of 3 to 4°C.

The major period of growth extended from about September to April with a possible growth restriction in the F-2 and/or earlier instar larvae during the period from January to April.

4.5. *PROCORDULIA SMITHII*

4.5.1. Lake Sarah - tb

4.5.1.1. Results From Fig. 21, small larvae first appeared during October 1976 (cohort 4) and March 1977 (cohort 5). The mean head width of cohort 4 (Fig. 22) increased at a uniform rate from November to March 1977. The mean head width was then 1.10mm, compared with 1.27mm for cohort 3 in March 1976.

The mean head width of cohort 3 increased slightly by the June sample (Fig. 22), but then little change occurred between June and September. From September the head width increased slowly until November and then at a higher rate until February 1977. Between February and March the mean head width increased markedly to 3.36mm, compared with 2.56mm for cohort 2 in March 1976.

Difficulty was experienced in separating cohorts 2 and 1 because the number of larvae in these cohorts was usually low. The average number of larvae in the monthly collections was 26 in cohort 2 and 14 in cohort 1. Therefore, the results for these cohorts must be regarded with reserve.

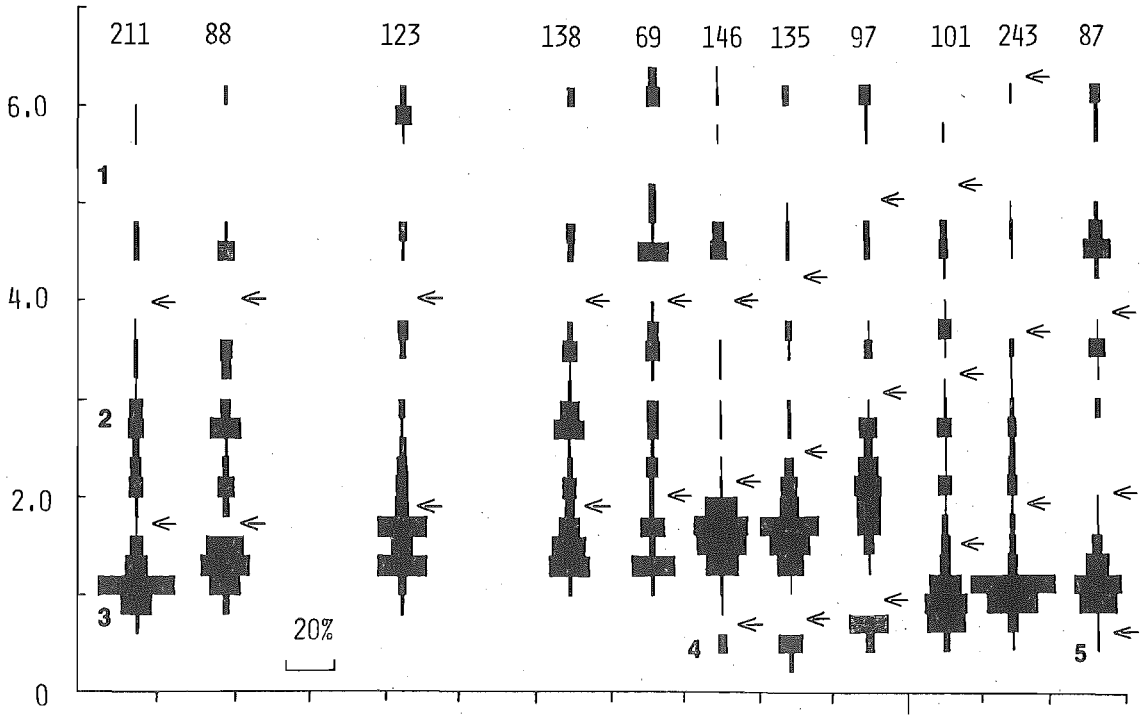
The mean head width of cohort 2 apparently increased from March to September, but then decreased in October (Fig. 22). From October the mean head width increased until February then remained constant until March 1977. The mean head width was then 4.94mm, compared with 4.25mm for cohort 1 in March 1976.

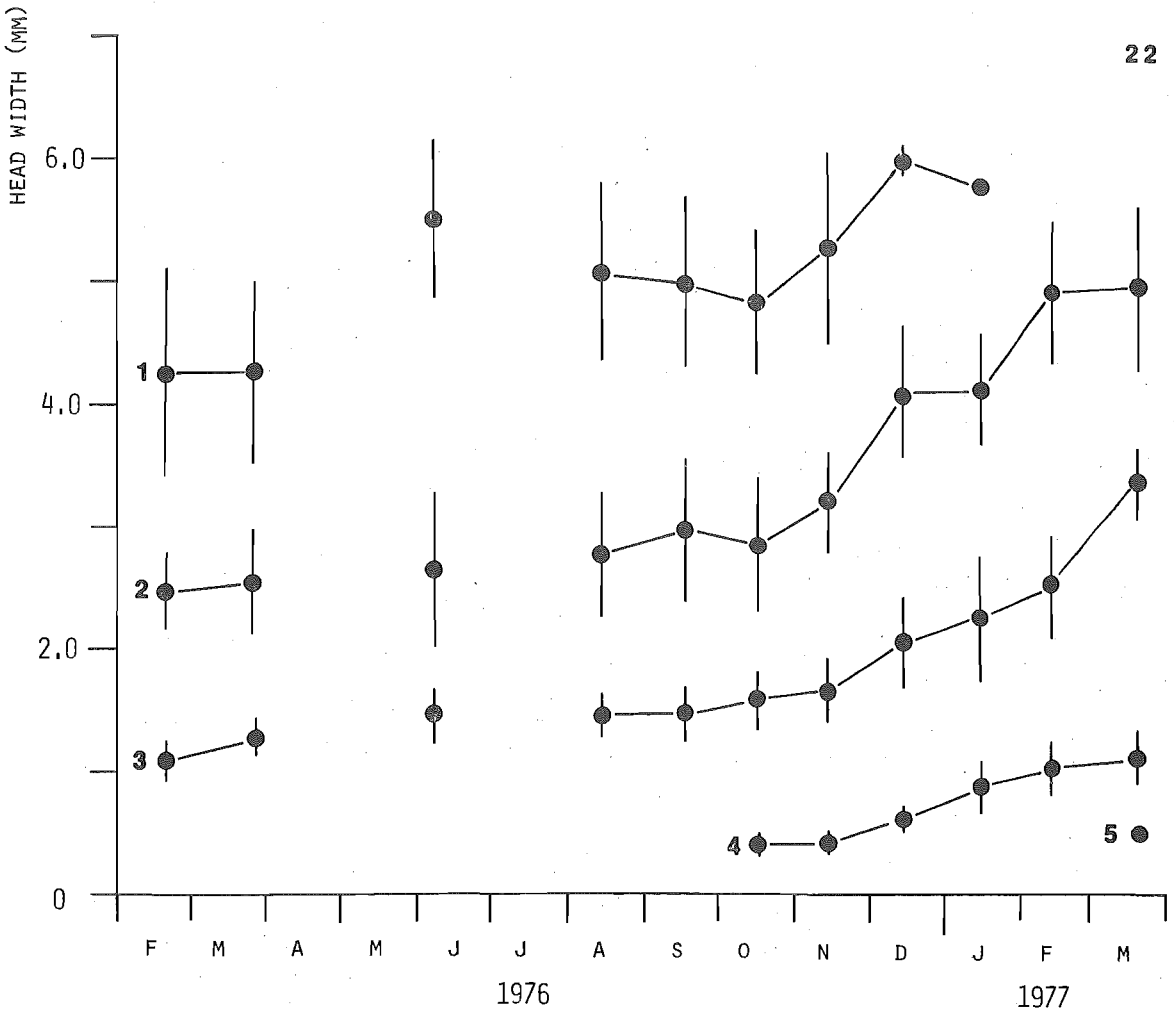
In cohort 1 little growth occurred between February and March 1976 (Fig. 22), whereas by the June collection the mean head width had increased markedly. However, by September it had decreased and continued to decrease until October. From October the mean head width increased until December, after which it decreased slightly in January 1977, immediately before the last of cohort 1 disappeared.

No trend was noted towards a decrease in the size of the F or F-1 instars during the warmer months (Fig. 21).

Fig. 21. Kite diagram showing head width size - class frequency distribution of *Procordulia smithii* larvae at Lake Sarah - tb. Sample size on each collection date indicated at top of graph. Arrows indicate region of separation or overlap between cohorts.

Fig. 22. Component cohorts of *Procordulia smithii* larvae in the population at Lake Sarah - tb. (Mean ± one standard deviation shown).


211
88
123
138
69
146
135
97
101
243
87
6.0
4.0
2.0
0
1
2
3
4
5
20%


HEAD WIDTH (MM)
6.0
4.0
2.0
0
1
2
3
4
5
F
M
A
M
J
J
A
S
O
N
D
J
F
M
1976
1977

In cohort 2 the F-1 instar larvae first appeared by December (Fig. 21) but the F instar larvae were not present until February. The sample size of cohort 2 at that time was n = 11 in December, n = 16 in January, and n = 6 in February.

4.5.1.2. Comments The appearance of small larvae (Fig. 21) during October 1976 and March 1977 was the first indication of the hatch of cohorts 4 and 5 respectively. The single, small larva (head width, 0.48mm) found in March 1977 was believed to represent cohort 5 because no small larvae were collected during either January or February. By March, the minimum head width in cohort 4 was 0.76mm. If the above larva was a member of cohort 5 then some hatching occurred the same summer that eggs were laid in 1977.

In cohort 4 no small larvae were found during February or March 1976. This indicated that either the eggs had not completed development until October in 1976, or hatching had occurred earlier than October but small larvae were not found until then. At Lake Sarah - tb small larvae of *X. zealandica* and *A. colensonis* (Figs. 17 and 19, respectively) were found consistently in the March, June and August 1976 samples and small larvae of *P. smithii* were found from October to November (Fig. 21). From this it seems probable that when small larvae are present in the field at least some are found in the samples, as is the case for cohort 5 in March 1977 (Fig. 21). Therefore, these results for cohort 4 are believed to indicate the start of a spring hatching period, similar to that of *A. colensonis* (section 4.4.1.2.). Recruitment of small *P. smithii* larvae ended by December which was believed to mark the end of the hatching period of cohort 4 in the field.

These results for cohort 4 indicate that the egg stage of *P. smithii* either requires a long incubation period, or has development interrupted by a dormancy period. Results for cohort 5 indicate that at least some eggs hatch the summer that they are laid. Therefore, from the above, most eggs hatch the summer following oviposition, but some eggs develop directly and hatch the same summer that they are laid. The reasons for this are examined in detail later (section 6.6.).

In cohort 3 the larvae were in approximately the same stage of development in March 1976 as the larvae in cohort 4 during the corresponding period in 1977. No growth occurred in cohort 3 from June to September, and not until October-November when the mean

monthly water temperature rose to 12.7°C was any appreciable increase in size noted. The marked increase in head width during March was attributed to variability caused by the small number of larvae (n = 10) in cohort 3 found in that collection.

In cohorts 1 and 2 the consistently low number of larvae found in the collections also resulted in considerable variability in the mean head width which was evident in their growth curves (Fig. 22). By smoothing these curves a pattern similar to that noted in cohorts 3 and 4 was obtained. Generally, growth started during October-November and continued at a uniform rate until March (cohort 2) or until cohort 1 disappeared from the population in January.

Cohort 2 was made up of F-2 to approximately F-4 instar larvae in March 1976. By March 1977 cohort 2 was then made up of F and F-1 instar larvae (Fig. 21).

Cohort 1 was also made up of F and F-1 instar in March 1976; however, the mean head width was much smaller than that of cohort 2 for the corresponding period in 1977. This was probably caused by a difference in growth seasons experienced by the two cohorts.

In cohort 1 a substantial moult into the F instar apparently occurred between March and June. However, the mean head width in June was unusually high when compared with the August and September samples, probably because of variability resulting from small sample size (n = 18). Therefore, the August and September samples were regarded as a better indication of the instar composition of cohort 1 during the winter. This was approximately 30% F and 70% F-1 instar larvae. As mentioned earlier, growth started about October and continued at a uniform rate until December. The presence of one small F instar larva in the January sample caused the deflection in the growth curve for that month.

The delayed appearance of the F instar in cohort 2 during December to February was interpreted as a possible indication of a growth restriction in F-1 instar larvae. However, because of the small sample sizes involved this cannot be established conclusively. Further discussion of larval growth restrictions in *P. smithii* is left for later sections (5.5.2.2. and 7.5.3.).

4.5.1.3. Summary At Lake Sarah - tb *P. smithii* has a four-year life cycle; however, it is possible that some larvae complete development in three years. The general pattern of development is as follows. Some eggs hatch the summer that they are laid but, for

undetermined reasons, hatching is not completed until the following summer. The first winter is spent mostly as eggs. About one year after oviposition (March) larvae have a head width of approximately 0.80 to 1.80mm. By March of the following year, about two years after oviposition, larvae have a head width of about 1.90 to 3.60mm, *i.e.* approximately the F-4 to F-2 instars. After the following summer, about three years after oviposition, larvae are in the F-1 and F instars. This group completes emergence by the end of the next summer, four years after oviposition. No growth occurred during the winter at mean water temperatures of 3 to 4°C. The major period of growth extended from October-November to March or possibly later in the F-1 instar larvae. A possible growth restriction occurs in the F-1 instar during the period from December to February.

5. EMERGENCE STUDY

5.1. INTRODUCTION

As mentioned at the start of the Field Study section, the emergence study was designed to describe the seasonality exhibited by each species and to provide an insight into the synchronisation involved in the appearance of the adult stage. In the past the seasonal pattern of emergence has been used effectively as an indicator of the degree to which a species is seasonally regulated. This use and its interpretation was described by Corbet (1964) and has been followed by various authors (*e.g.*, Lutz & McMahan 1973; Ubukata 1973; Ingram & Jenner 1976b). Two types of seasonal emergence patterns have been recognised for the Odonata. One pattern shows a burst of emergence at the start of the emergence period, followed by a sharp decrease in the rate of emergence. The other pattern shows a relatively constant rate of emergence throughout the emergence period. These correspond to the general seasonal emergence patterns shown by 'spring' and 'summer' species, respectively (see Corbet & Corbet 1958).

Aspects of emergence treated in this section include:

- the diel pattern of emergence;
- the seasonal pattern of emergence; and
- (if possible) the appearance of the sexes within the emergence period, as well as the overall sex ratio.

The diel pattern of emergence was examined for two reasons, firstly to determine the period of the day during which emergence takes place and secondly to evaluate the effect that regular collections of exuviae have on the progress of emergence.

The seasonal pattern of emergence was examined and described for use as an indicator of seasonal regulation. An attempt was made to correlate the emergence pattern of *X. zealandica*, from site to site and year to year, with various environmental parameters, especially those related to altitude.

The appearance of the sexes within the emergence period was examined to determine the possible influence on the overall seasonal pattern of emergence. The sex ratio was determined as an offshoot of this study.

5.2. TECHNIQUES

5.2.1. Diel Pattern of Emergence

The diel pattern of emergence from selected areas was followed at Isaac's Pond and Lake Sarah - tb. The areas were selected so as not to interfere with regular exuviae collections. The areas were cleared of exuviae late on the evening preceding the diel study and a final check was made just prior to sunset to determine whether emergence was in progress at that time. Collections were started before sunrise on the day of the study and were continued at intervals as specified in the results sections. The air temperature, taken in the shade with a shielded, bulb thermometer about 0.5m above the water, was recorded at the start of each check and cloud cover was noted. The study was terminated when no further larvae were found emerging at the selected areas.

5.2.2. Seasonal Pattern of Emergence

The seasonal pattern of emergence for *X. zealandica* and *A. colensonis* was established by collections of exuviae (modelled after Corbet 1957b) at the Isaac's Pond site (Fig.10) from the same strip of *J. gregiflorus* (1.0m wide by 2.0m long) along the margin of the channel during 1975-1976, 1976-1977 and 1977-1978. At Lake Sarah collections were made from the same areas at the two sites (Fig.11) during 1976-1977 and 1977-1978. The pattern of emergence for the zygopterans and *P. smithii* was established at Lake Sarah - tb and for the zygopterans and *P. grayi* at Lake Sarah - ls.

The Lake Sarah - tb emergence site consisted of:

- three plots of *T. orientalis* (one plot 2.0m wide by 2.0m long and two plots 1.5m wide by 1.5m long); and
- six groups of smooth, wooden dowels (20 dowels to a group) representing artificial emergence sites as described by Ingram (1976b). Each dowel (1.0m long by 10mm in diameter) extended about 0.5m above the water.

The Lake Sarah - ls emergence site consisted of a strip of *S. pauciflorus* (1.0m wide by 7.0m long) along the lake shore.

The pattern of emergence from these three sites is considered to be representative of natural larval populations. The aquatic habitat

in or around any of the emergence sites was left undisturbed throughout this study. Also, because exuviae collections were made from the same sites from year to year, the results obtained are considered to be directly comparable from year to year.

At Isaac's Pond during 1975-1976, collections were made between 13:00 and 16:00 Solar Time (for time notation see section 3.3.3.). In subsequent years, at all the sites, collections were made between 11:00 and 14:00. This change was necessary to accommodate standard collection times at both Isaac's Pond and Lake Sarah. For the effect that collection time had on the progress of emergence see sections 5.3.1., 5.4.1., 5.5.1., 5.6.1. .

At Isaac's Pond during 1975-1976 the interval between collections was two days, ranging from one to four days on a few occasions. At all the sites during subsequent years, collections were made at approximately weekly intervals, ranging from four to ten days. Some exuviae were dislodged by wind and rain but this was considered not to alter the overall pattern of emergence. Because collection intervals were kept as constant as possible the loss of exuviae for each species was assumed to be constant, although it varied from species to species.

Tests, carried out at the sites using freshly deposited exuviae, showed a cumulative loss for *X. zealandica* (combined n = 33) of about 20% during the first week which increased to about 30% by the end of the second week. For *A. colensonis* (combined n = 26) the cumulative loss was slightly higher, perhaps because of the larger, more fragile exuviae of this species. About 30% were dislodged during the first week and about 40% by the end of the second week.

Loss was higher from exposed sites than from sheltered sites. Depending on the nature of the site, exuviae were occasionally found at the base of the plants from which they had been dislodged. A few exuviae of the zygopterans remained *in situ* for about 220 days and were still recognisable at the start of the new emergence period.

No tests were carried out using exuviae of the *Procordulia* species, but the loss rate was probably similar to that observed for the zygopterans. The exuviae of both *Procordulia* species were often so firmly attached to the emergence site that the legs had to be broken before the exuviae could be removed. Some old exuviae of *P. smithii* and *P. grayi* were found *in situ* at the end of winter. These had been

there at least nine to ten months, from the end of emergence the previous summer.

These tests showed that loss of exuviae occurred during the interval between collections, up to 30% for *A. colensonis* during a one week period. Some of the dislodged exuviae were found amongst the vegetation; therefore, the loss rates obtained probably represented maximum values. Because the collection intervals were kept relatively constant, the overall pattern of emergence was probably affected only slightly; however, the number of exuviae collected was always underestimated.

Careful collections were made to remove the old exuviae at the various sites before the start of emergence. Old exuviae of all the species were extremely brittle; also, they appeared bleached and often they were broken.

Metamorphosis of final instar larvae taken in larval collections was used to predict the start of emergence; therefore, regular exuviae collections were started before emergence began. Only at Isaac's Pond in 1975 was the start of emergence not observed. Emergence actually started between the date of the last zero collection of exuviae and the date of the first collection of exuviae followed by continuing emergence. Regular collections were made at least twice after the last exuviae were collected. Emergence actually ended between the dates of the penultimate and final collection of exuviae followed by zero emergence.

At Isaac's Pond in 1976 collections were continued at weekly intervals from the end of emergence to the start of the following emergence period, hereafter referred to as the 'off-season'. At all the sites in 1977, and at Isaac's Pond in 1978, collections were made at monthly intervals during the 'off-season'.

5.2.3. Sex Determination and Preservation of Exuviae

The exuviae were returned to the laboratory in a dry state, then moistened with water which softened the cuticle and helped to prevent breakage during examination. A Wild M5 dissecting microscope at 25X magnification was used to facilitate identifications and sex determinations.

The sexes of the exuviae of the zygopterans were determined by examination of external genitalia. Females have a rudimentary ovipositor on the eighth and ninth abdominal sternites. Males have two small spines on the ninth abdominal sternite and faint markings on the second abdominal sternite. Exuviae with missing abdominal segments could still be sexed as long as they possessed the second abdominal sternite. Exuviae without at least the second abdominal sternite were not counted in the sex ratio.

Characteristics could not be found to allow the positive determination of the sexes of the exuviae of the *Procordulia* species. No sex ratio information is presented for these two species.

All exuviae were retained for possible future reference. They were stored in 70% alcohol plus 1% glycerine which kept the cuticle soft and helped to prevent breakage.

5.2.4. Analyses of Results and Definition of Terms

The results are usually presented in a graphical form. The diel pattern of emergence is plotted in a cumulative fashion on a natural scale. The seasonal pattern of emergence is also plotted in a cumulative fashion on a natural scale and then is presented as a cumulative emergence line (see Corbet & Danks 1973) showing the points of $EM_{0,\ 10,\ 50,\ 90}$ and $_{100}$. This terminology *e.g.* $EM_{50,}$ is modelled after the definition of Taketo (1960). He defined EM_{50} as "the time by which half of the annual emergence is reached". This can be easily visualised on the emergence lines (*e.g.* Fig. 28) and also is summarised as calendar dates presented in tabular form. I use calendar dates instead of time in days, because the former notation facilitates the comparison of emergence from year to year and site to site.

The range in the start and the end of emergence is marked on the cumulative emergence line and given in the tables; however, the duration of emergence for this study is considered to include the entire period between the last zero check before the start of emergence, (EM_0) and the final collection of exuviae at the end of emergence (EM_{100}). This is the maximum possible duration of emergence as it includes the ranges at the start and the end of emergence.

The use of the terminology $EM_0{}^{10}$, *etc.* is modelled after $EM_{10}{}^{90}$ as used by Ubukata (1974). He defined $EM_{10}{}^{90}$ as "the interval in days

between two dates by which respectively 10 and 90% of the annual population emerged.". I use this notation to denote intervals within the emergence period because it is an easy form of reference that is readily understood.

The emergence pattern was analysed for polymodality using the Cassie technique (Cassie 1950, 1954). The annual emergence was plotted in a cumulative fashion on arithmetic probability paper when the sample size was greater than 49. A modified probability paper technique was used when the sample size was less than 50 (Harding 1949). The date of EM_{50} of each mode and the percent of the total annual population that each mode composed was determined.

The sex ratio at emergence was determined and the pattern of the appearance of the sexes graphed.

5.3. *XANTHOCNEMIS ZEALANDICA*

5.3.1. Diel Pattern of Emergence

5.3.1.1. Results During collections of exuviae from the various sites, larvae in the process of emergence and teneral adults were encountered more frequently before solar noon than after. The diel pattern of emergence was examined in special studies that were made at Lake Sarah - 1s on 24 January 1977 and at Isaac's Pond on 9 February 1978. These studies did not interfere with the regular collection of exuviae. At Lake Sarah - 1s hourly collections of exuviae were made starting before sunrise and continued to the end of emergence. The pattern of emergence is presented in Fig. 23. At Isaac's Pond hourly collections were made starting before sunrise and continued up to solar noon when I had to leave the study area to return material to the laboratory. Additional collections were made in the evening to determine if emergence had ended. The pattern of emergence is presented in Fig. 24.

The diel pattern of emergence was similar on both occasions. Emergence started only after sunrise. Some individuals emerged at an air temperature at least as low as 10°C. The maximum rate of emergence was observed within a few hours of sunrise with about 80% of the daily emergence completed by solar noon.

Additional observations, made during the nights of the 8th and 28th January 1978 at Lake Sarah - 1s, showed no emergence of

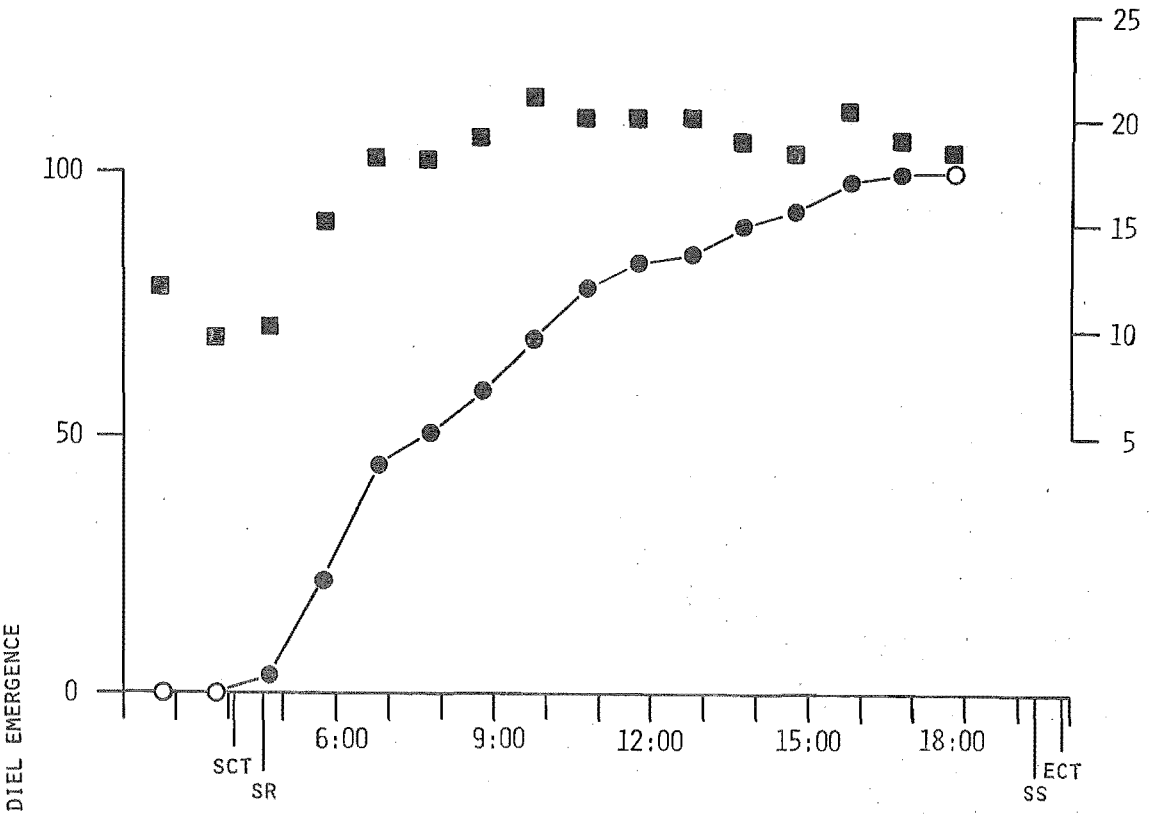
Fig. 23. Diel pattern of emergence of *Xanthocnemis zealandica* at Lake Sarah - 1s, 24 January 1977. Sample size; n = 82.

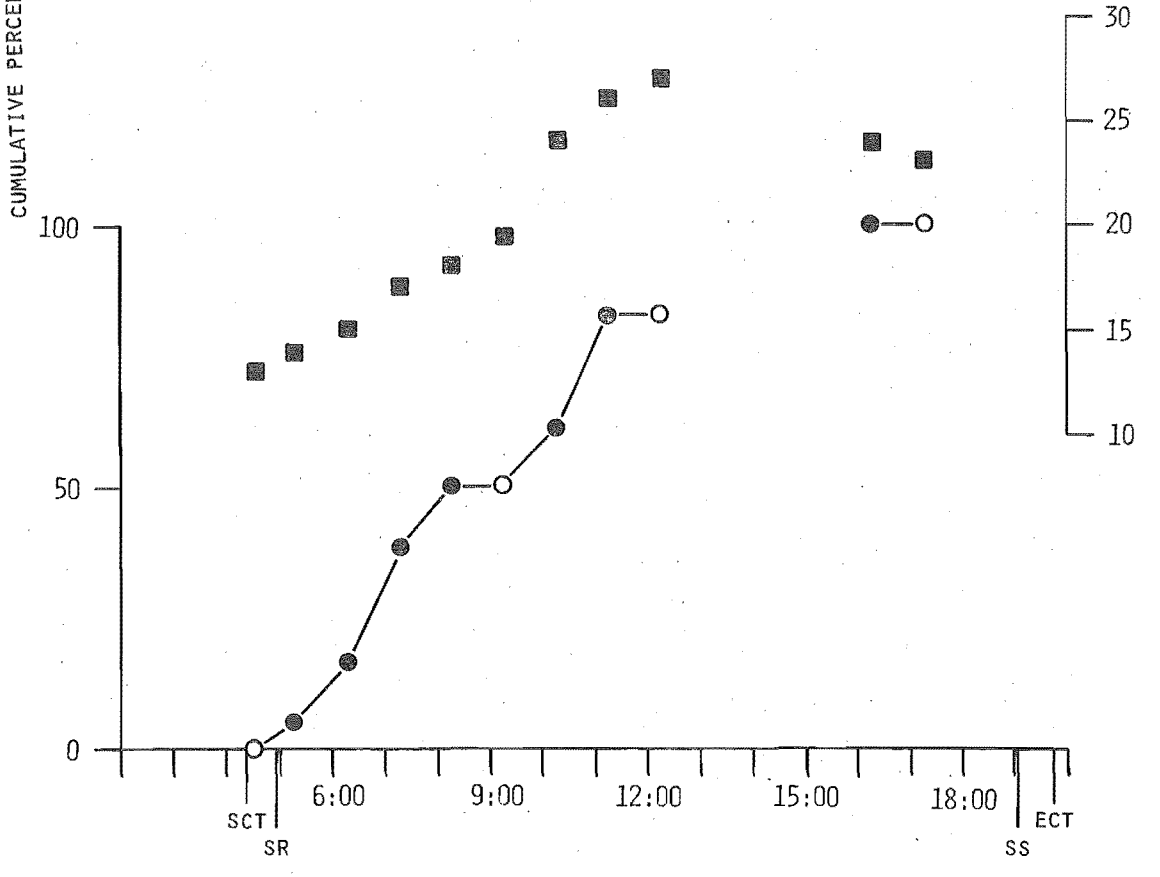
Fig. 24. Diel pattern of emergence of *Xanthocnemis zealandica* at Isaac's Pond, 9 February 1978. Sample size; n = 18.

For Figs. 23 & 24 the number emerged included all individuals in the process of eclosion plus the exuviae left *in situ* during the interval between collections.

Abbreviations to Figs. 23 & 24.

hollow circle	-	no emergence by time of collection
solid circle	-	emergence in progress
square	-	air temperature at time of collection
ECT	-	end Civil Twilight
SCT	-	start Civil Twilight
SR	-	sunrise
SS	-	sunset





CUMULATIVE PERCENTAGE OF DIEL EMERGENCE

AIR TEMPERATURE (°C)

SOLAR TIME

X. zealandica before sunrise.

5.3.1.2. Comments *X. zealandica* apparently emerges only during daylight hours and completes most of the daily emergence before solar noon. Usually exuviae collections were made after solar noon (section 5.2.2.) at a time when the daily emergence was almost completed. Therefore, the regular collections of exuviae had a slight effect only on the progress of emergence.

The emergence observed during the early morning (Fig. 23) indicates that *X. zealandica* can emerge at temperatures at least as low as 10°C. Cloud cover apparently had little effect on emergence. No increase or decrease in the rate of emergence occurred in response to changes in cloud cover.

5.3.2. Seasonal Pattern of Emergence

5.3.2.1. Results The general pattern of emergence of *X. zealandica* (Figs. 25 to 27) shows a relatively constant rate of emergence throughout the emergence period (EM_{10}^{90}) with a slow increase and decrease in the rate at the start (EM_{0}^{10}) and at the end (EM_{90}^{100}), respectively. No synchronisation of emergence within the emergence period is evident.

Emergence began by widely differing dates at the various sites, but the end of emergence was similar (Table 9). The dates of $EM_{0,\ 10}$ and $_{50}$ (Fig. 28, Table 9) were similar from year to year at a given site, but varied from site to site. The dates of EM_{90} and especially EM_{100} were similar at all the sites during all the years of the study.

The date of EM_0 was not observed at Isaac's Pond in 1975. Any loss of exuviae from the emergence site between the start of emergence and 28 September when regular exuviae collections were started would affect the total number of exuviae collected during 1975-1976. Because this total was used to calculate the EM dates (Fig. 28, Table 9), the dates of $EM_{10,\ 50}$ and $_{90}$ are approximations; only that of EM_{100} is accurately known (see pp. 73-74).

The mean water temperature for the week during which emergence started (Table 9) ranged from 10 to 12°C at all the sites.

During the 'off-season' one exuvia was collected at Isaac's Pond and none at the Lake Sarah sites. The emergence of the individual at Isaac's Pond took place between 27 June and 5 July 1976.

The total number of exuviae collected each year (Table 9) was

Fig. 25. Cumulative percentage of *Xanthocnemis zealandica* emerged at Isaac's Pond during 1975-1978.

Fig. 26. Cumulative percentage of *Xanthocnemis zealandica* emerged at Lake Sarah - tb during 1976-1978.

Fig. 27. Cumulative percentage of *Xanthocnemis zealandica* emerged at Lake Sarah - ls during 1976-1978.

List of symbols for Figs. 25 to 27.

Hollow symbol	-	no exuviae found
square	-	1975-1976
circle	-	1976-1977
triangle	-	1977-1978

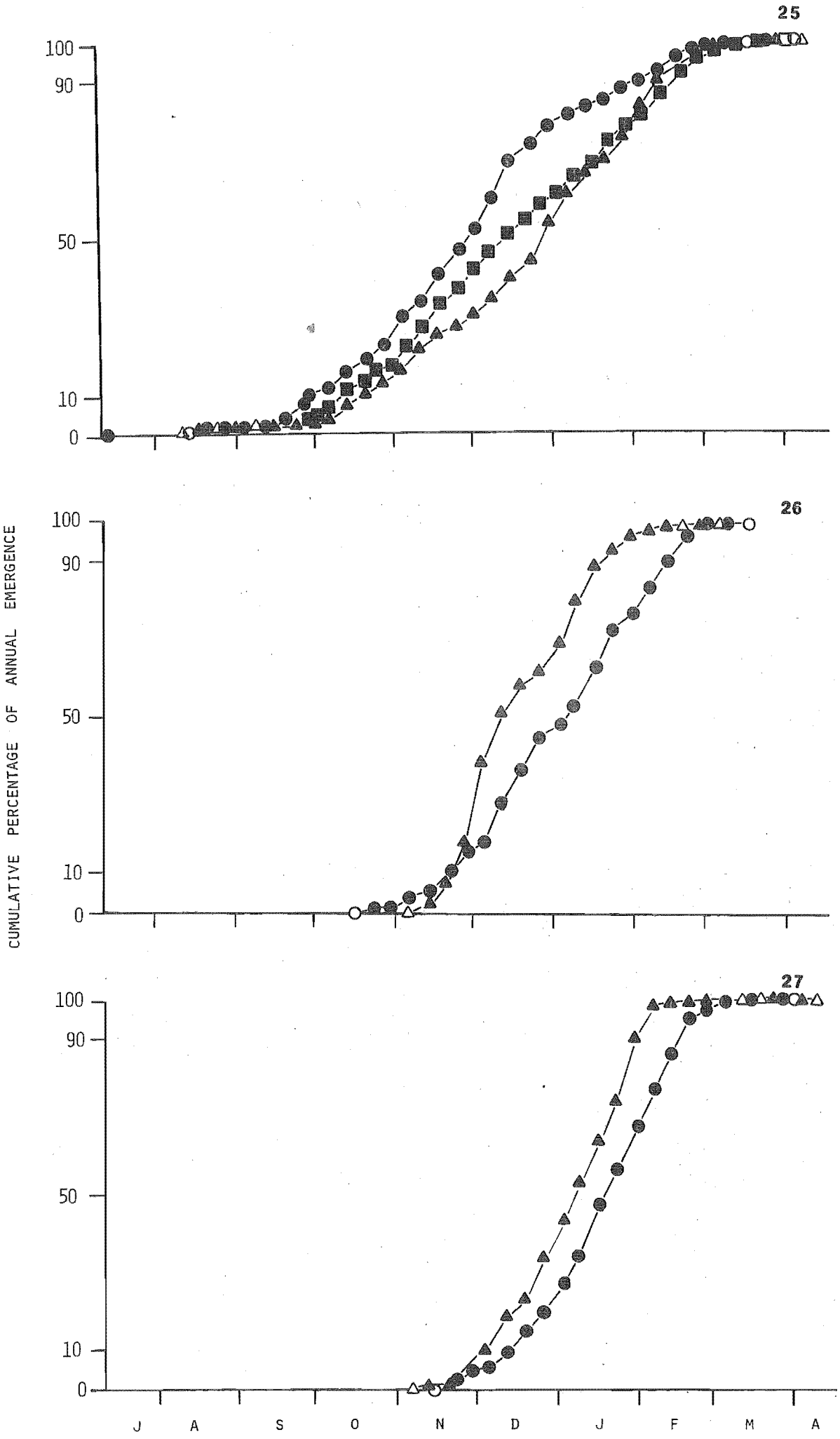

25
26
27
100
90
50
10
0
CUMULATIVE PERCENTAGE OF ANNUAL EMERGENCE
J
A
S
O
N
D
J
F
M
A

TABLE 9 SUMMARY OF EMERGENCE RESULTS FOR *XANTHOCNEMIS ZEALANDICA*

Study Site	Emergence Period	Number of Exuviae	Dates of Specified EM Points EM_0	EM_{10}	EM_{50}	EM_{90}	EM_{100}	Duration of Emergence (Days)	Combined Range of EM_0 and EM_{100} (Days)	Mean Water Temperature (°C) at EM_0
	1975-1976	967	In Progress 28 Sept	12 Oct	10 Dec	17 Feb	17-19 Mar	>173	-	-
	One female collected 5 July 1976									
Isaac's Pond	1976-1977	1658	13-19 Aug	2 Oct	29 Nov	1 Feb	16-23 Mar	222	13	11 1/2
	1977-1978	793	11-17 Aug	21 Oct	27 Dec	9 Feb	17-24 Mar	225	13	10
	1978-1979		16-20 Aug	One male and one female collected						
Lake Sarah - tb	1976-1977	618	16-24 Oct	21 Nov	3 Jan	14 Feb	27 Feb -6 Mar	141	15	12
	1977-1978	344	6-14 Nov	22 Nov	13 Dec	19 Jan	19-26 Feb	112	15	10 1/2
Lake Sarah - ls	1976-1977	4322	14-22 Nov	12 Dec	18 Jan	16 Feb	16-20 Mar	126	12	-
	1977-1978	5046	6-14 Nov	3 Dec	6 Jan	29 Jan	26 Mar -2 Apr	147	15	12

Fig. 28. Cumulative emergence lines of *Xanthocnemis zealandica*. For sample size see Table 9. Hollow circles indicate the range in the start and end of emergence (see text).

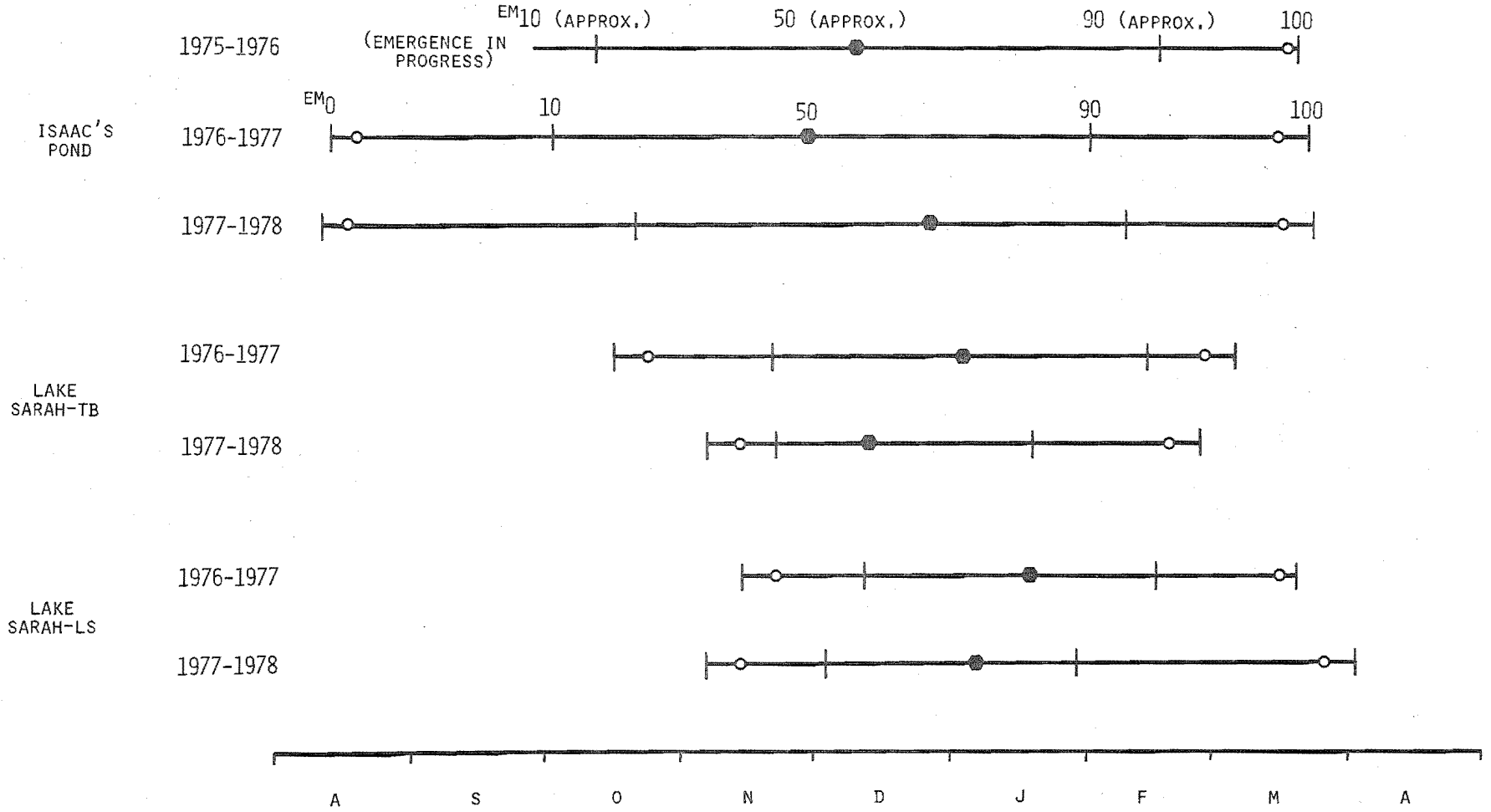

EM10 (APPROX.)
50 (APPROX.)
90 (APPROX.)
100
1975-1976
(EMERGENCE IN PROGRESS)
EM0
10
50
90
100
ISAAC'S POND
1976-1977
1977-1978
1976-1977
LAKE SARAH-TB
1977-1978
1976-1977
LAKE SARAH-LS
1977-1978
A
S
O
N
D
J
F
M
A

Fig. 29. Cumulative percentage of *Xanthocnemis zealandica* emerged at Isaac's Pond, 1976-1977 (Abscissa on probability scale), n = 1658.

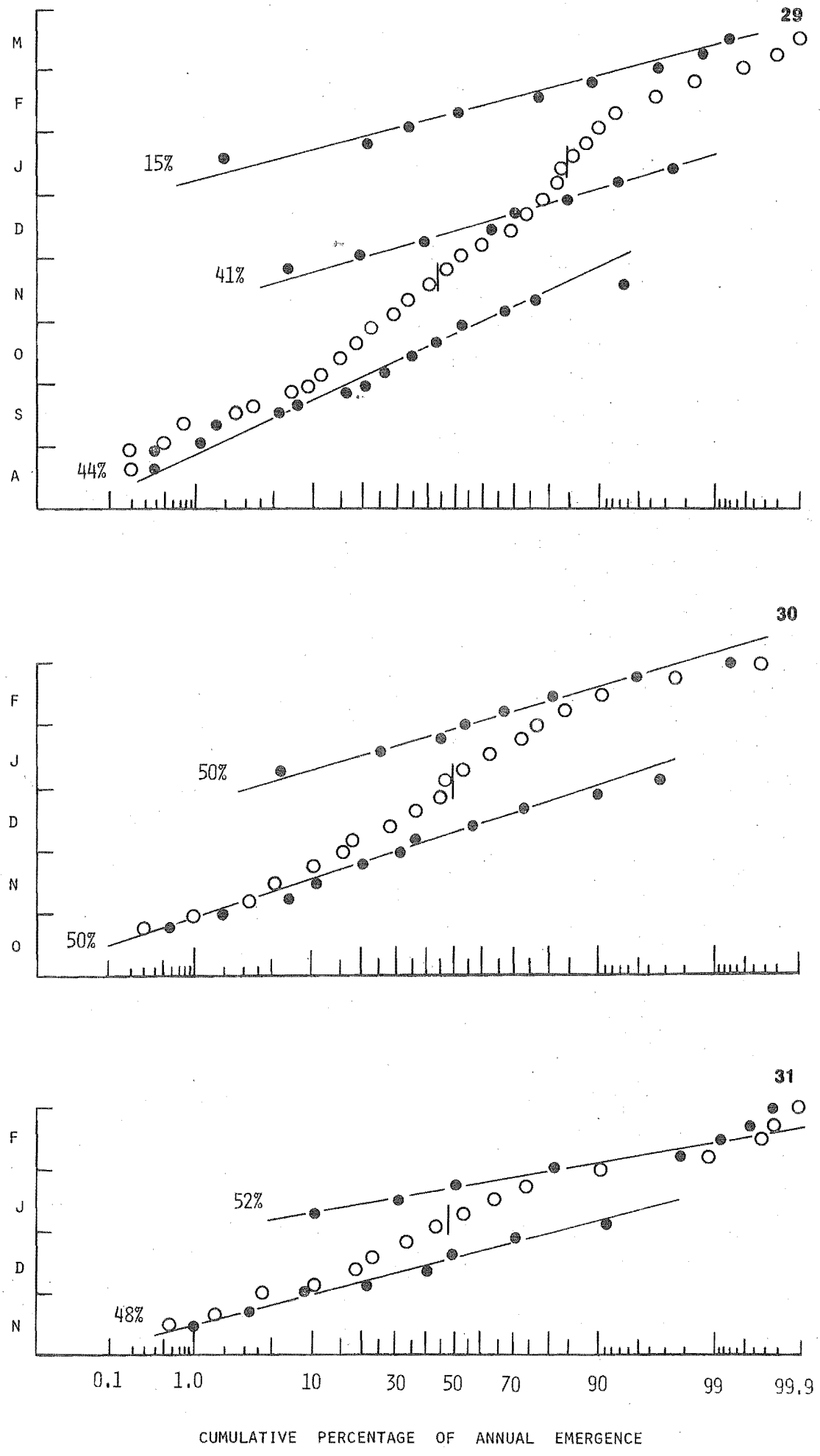
Fig. 30. Cumulative percentage of *Xanthocnemis zealandica* emerged at Lake Sarah - tb, 1976-1977 (Abscissa on probability scale), n = 618.

Fig. 31. Cumulative percentage of *Xanthocnemis zealandica* emerged at Lake Sarah - ls, 1977-1978 (Abscissa on probability scale), n = 5046.

List of symbols for Figs. 29 to 31.

hollow - original distribution

solid - derived modes.


29
M
F
J
D
N
O
S
A
15%
41%
44%
30
F
J
D
N
O
50%
50%
31
F
J
D
N
52%
48%
0.1
1.0
10
30
50
70
90
99
99.9
CUMULATIVE PERCENTAGE OF ANNUAL EMERGENCE

about the same at Lake Sarah -ls but varied considerably at Isaac's Pond and Lake Sarah - tb. Substantially more individuals emerged during 1976-1977 at the latter sites.

Polymodality analyses consistently showed the emergence pattern of *X. zealandica* to be trimodal at Isaac's Pond (*e.g.* Fig. 29) and bimodal at both the Lake Sarah sites (*e.g.* Figs. 30 & 31). Table 10 presents the calculated date of EM_{50} of each mode and the percentage of the total annual population that each mode composed.

TABLE 10. Modality of emergence of *Xanthocnemis zealandica*.

		MODE 1		MODE 2		MODE 3	
		Date EM_{50}	Percent of Annual Population	Date EM_{50}	Percent of Annual Population	Date EM_{50}	Percent of Annual Population
Isaac's Pond	1975-1976	7 Oct	16	25 Nov	44	31 Jan	40
	1976-1977	24 Oct	44	15 Dec	41	8 Feb	15
	1977-1978	28 Oct	28	23 Dec	40	4 Feb	32
Lake Sarah-tb	1976-1977	5 Dec	49	29 Jan	51	-	-
	1977-1978	30 Nov	50	10 Jan	50	-	-
Lake Sarah-ls	1976-1977	30 Dec	49	5 Feb	51	-	-
	1977-1978	16 Dec	48	21 Jan	52	-	-

5.3.2.2. Comments The approximations of the EM dates of *X. zealandica* at Isaac's Pond during 1975-1976 were similar to results for subsequent years at that site (Table 9), as was the pattern of emergence (Fig. 25). This may indicate that the 1975-1976 results are relatively reliable. Results for the following years indicated that only a small percentage of the total annual population emerged before the end of September, about 7.4% and 2.0% in 1976-1977 and

1977-1978, respectively. If a similar percentage emerged during this period in 1975-1976 and only some of the exuviae were lost, then the effect on the total number of exuviae collected was slight. Therefore, the approximations of the dates of $EM_{10, 50}$ and $_{90}$ are close to the true values.

Rising water temperature is unlikely to determine the start of emergence. Mean weekly water temperatures of 10°C or higher were recorded at Isaac's Pond during the 'off-season' and at Lake Sarah - tb during October with no occurrence of emergence. For example, at Lake Sarah - tb during each of the three weeks prior to the start of emergence for 1977-1978, a mean weekly water temperature of 10°C or more was recorded.

The start of emergence appeared to be dependent on the 'off-season' water temperature regimen. Emergence started during August at Isaac's Pond, about 100 days earlier than at the Lake Sarah sites. During April to August Isaac's Pond experienced mean monthly water temperatures (Fig. 12) that were about 6°C higher than at Lake Sarah -tb (Fig. 13). The warmer water temperature regimen at Isaac's Pond probably promoted development within the final instar which resulted in the earlier start of emergence from that site.

The emergence at Isaac's Pond that took place between 27 June and 5 July 1976 was probably related to temperature conditions experienced during that year (see sections 3.3.2.1. and 3.4.). The water and especially the air temperatures recorded for the 'off-season' of 1976 were higher than the corresponding values for 1977 (Fig. 12). The maximum air and water temperature for the week during which emergence took place was 16°C and 11°C respectively. Higher air and water temperatures were recorded both before and after the emergence of 5 July but no additional emergence was observed. The isolated emergence must have resulted from the exposure of this individual to unusually warm conditions experienced in the shallow, sheltered water found at the base of the *J. gregiflorus*. Therefore, the emergence of additional individuals could have been expected at Isaac's Pond during this period, whereas the low temperatures experienced at Lake Sarah made 'off-season' emergence extremely unlikely.

The site to site variation of EM dates decreased through the emergence period. The least variation was shown in the date of EM_{100}

(Table 9) which usually occurred within a two week period centred around 20 March. The date of EM_{100} at Lake Sarah - tb showed the greatest variation (Fig. 28), probably because of the variability of the physical and chemical conditions at this site. For example, the drying out of the collection sites during 1978 (section 3.3.4.2.) may have killed the remaining population that was destined to emerge that season, thereby terminating emergence prematurely.

The similarity of the date of EM_{100} from site to site and from year to year is believed to support the hypothesis that some form of restriction occurs in the F-3 to F instar larvae (see sections 4.3.1. and 4.3.2.). The water temperature at the end of emergence was still high enough (10-12°C) to permit the continuation of emergence, and remained so until May or June at Isaac's Pond (Fig. 12) and April at Lake Sarah - tb (Fig. 13). The growth restriction first prevented moulting into the F instar during January and February, and later prolonged the development of F instar larvae; therefore, emergence ended by March at both sites.

These factors indicate a dormancy period, probably diapause, that occurs in later instar larvae. Dormancy took place during mid-summer and emergence ended by approximately the same date at all the sites; therefore, the inducing agent was probably photoperiod. As noted earlier (section 3.4.) the temperature regimen differed markedly between Isaac's Pond and the Lake Sarah sites, whereas the photoperiod regimen was almost identical.

The variation in the number of exuviae collected at each site from year to year was probably a normal component of the population dynamics of this species. The emergence sites were disturbed as little as possible and no larval collections were taken from the areas. The maximum number of exuviae collected at Isaac's Pond was obtained during the second year of study, 1976-1977 (Table 9), indicating that the number of exuviae collected was not related to collecting techniques.

The different modality of emergence observed at Isaac's Pond and the Lake Sarah sites is perhaps a reflection of the different larval growth patterns at the sites (sections 4.3.1. and 4.3.2.). At Isaac's Pond, *X. zealandica* has a two-year life cycle, whereas at Lake Sarah - tb it has a three-year life cycle. During the years of the larval study the emerging cohort at the first site was composed of approximately the last six instars at the start of emergence in

August (section 4.3.1.2. p.45). At Lake Sarah - tb in October 1976 the emerging cohort was made up of the last four instars at the start of emergence (section 4.3.2.2. p.50). A comparison of the percentage composition of these instars within the emerging cohort at the start of emergence with the percentage composition of each mode within the seasonal pattern of emergence (Table 10) was carried out to determine if a trend was noticeable.

At Isaac's Pond in 1975 the first mode was made up of part of the F instar group and in 1976 it was made up of a combination of F and F-1 instar larvae. In both years the second mode was apparently composed of F-1 and F-2 instar larvae and the third mode was composed of F-3 to F-5 instar larvae. The relative size of this last group corresponded well with the relative size of the third mode; 37.7% and 40%, respectively in 1975-1976 and 13.1% and 15% in 1976-1977.

At Lake Sarah - tb in 1976-1977 the comparison of instar composition with modal groups showed a close similarity. The first mode (49%) was made up of F and F-1 instar larvae (54.3%) and the second mode (51%) was made up of F-2 and F-3 instar larvae (45.7%).

At Isaac's Pond the percentage composition of each modal group in the emerging population varied from year to year (Table 10). This appeared to be related to conditions during the 'off-season' that were experienced by the cohort destined to emerge. During the mild winter of 1976 (section 3.4.) larvae continued to grow and develop at a relatively high rate (Fig. 16) which resulted in a large first modal group and a small third modal group. The winter of 1977 was more severe (section 3.4.); therefore, the first modal group was smaller and the third modal group was larger. No direct information was available on the winter conditions at Isaac's Pond during 1975; however, from the emergence results for that period (Table 10) it was inferred that the winter of 1975 was more severe than that of 1977. The mean air temperature for the period from June to August, calculated from meteorological observations at the Christchurch International Airport, was 5.9°C in 1975 and 6.1°C in 1977. This is believed to support the above conclusion.

At the Lake Sarah sites little change occurred in the relative size of each modal group in the emerging population from year to year (Table 10). This similarity of modal group sizes at sites which experienced different temperature regimens (section 3.4.) was

interpreted as follows. The combination of a summer dormancy followed by a relatively cold winter results in a similar instar composition in the emerging cohort by the start of the emergence period at both sites each year. Therefore, the modality of emergence would remain similar from year to year; however, the timing of emergence would still vary depending on the current ambient temperature.

5.3.3. Sex Ratio

5.3.3.1. Results The sex ratio and pattern of appearance of the sexes was determined only from the exuviae collected at Isaac's Pond and Lake Sarah - 1s during 1976-1977 and 1977-1978. The emergence obtained from these sites during these two seasons was considered to be representative for this species.

Table 11 presents the sex ratios based on the complete emergence period which show male excess to be slight but consistent. Figures 32 & 33 show the changing proportion of males in the population during the emergence period. Females emerge earlier in the season than males, but by the end of emergence males predominate overall.

TABLE 11. Sex ratios of *Xanthocnemis zealandica* based on collections of exuviae at Isaac's Pond and Lake Sarah - 1s during 1976-1977 and 1977-1978.

		Total Number Collected	Number Unsexed	Number of Males	Percent Males
Isaac's Pond	1976-1977	1658	23	827	50.6
	1977-1978	793	20	397	51.4
Lake Sarah - 1s	1976-1977	4322	52	2184	51.1
	1977-1978	5046	63	2502	50.2

5.3.3.2. Comments These observations add to the literature four sex ratio records for one species. The records were based on exhaustive collections of exuviae made throughout the entire emergence

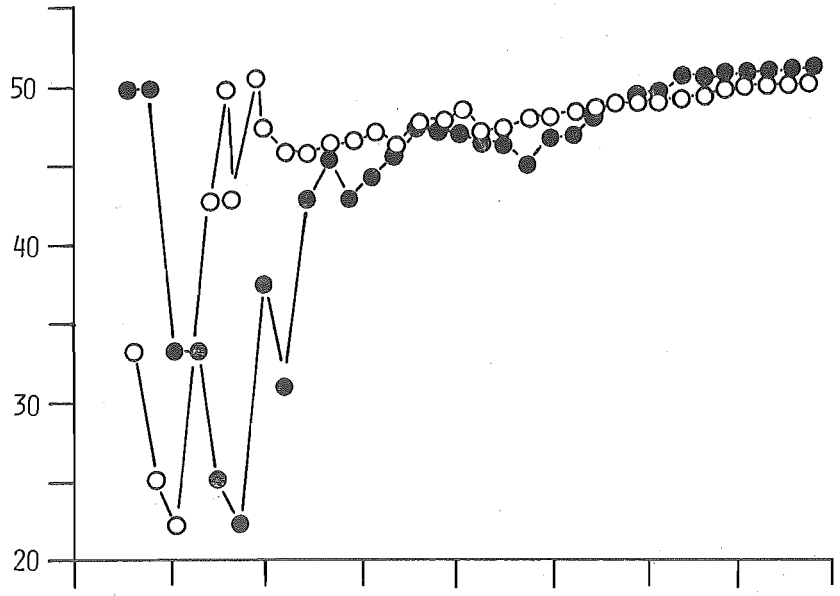
Fig. 32. Cumulative percentage of *Xanthocnemis zealandica* males emerged during annual emergence at Isaac's Pond (1976-1977 and 1977-1978).

Fig. 33. Cumulative percentage of *Xanthocnemis zealandica* males emerged during annual emergence at Lake Sarah - ls (1976-1977 and 1977-1978).

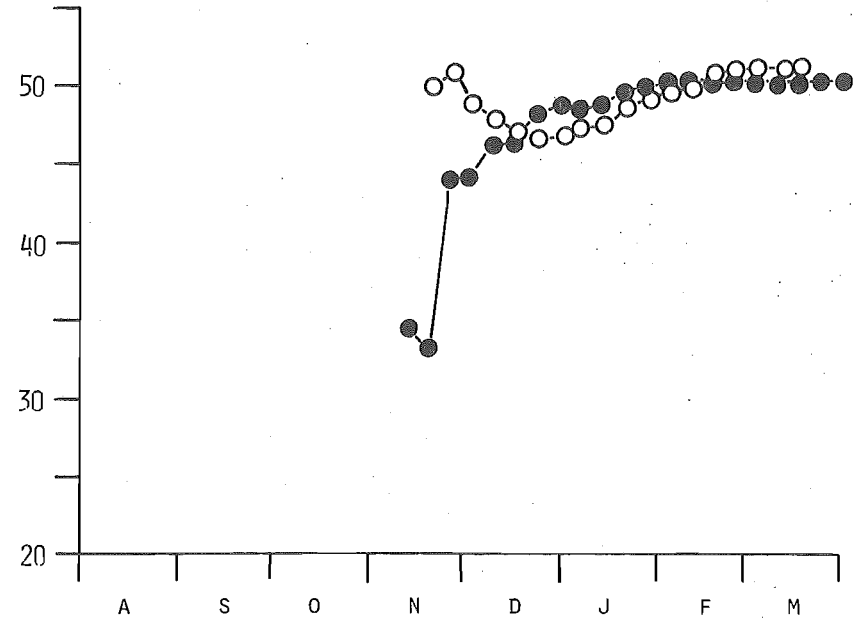
List of symbols for Figs. 32 & 33.

- hollow symbol 1976-1977
- solid symbol 1977-1978

CUMULATIVE PERCENTAGE OF MALES EMERGED DURING ANNUAL EMERGENCE



32



33

period. These results combined with previous work on the Zygoptera of a comparable nature (Lutz 1968a; Lawton 1972; Ingram 1976b; Ingram & Jenner 1976b) indicate that male predominance in the sex ratio may prevail in the Zygoptera, whereas female excess is more common in the Anisoptera (Corbet 1962).

Observations on the pattern of appearance of the sexes within the emergence period made by Fernet & Pilon (1971) indicated that females emerged earlier than males in *Enallagma boreale* Selys and *Enallagma vernale* Gloyd, two coenagrionids. A similar trend was noted in *X. zealandica*, possibly indicating a recurring pattern for the family. The cause of this changing proportion of sexes during the emergence period, or of an excess of one sex is unknown.

5.3.4. Summary

X. zealandica emerges predominantly during the morning shortly after sunrise.

The start of seasonal emergence is dependent on temperatures experienced during the winter and spring, not on a thermal threshold. There is no evident synchronisation of emergence within the emergence period, although the end of emergence apparently is the result of a summer dormancy in the later instar larvae.

At Isaac's Pond mild winter conditions and a relatively wide range of instars in the emerging cohort result in a long emergence period, with three modal groups that vary in size from year to year.

At Lake Sarah the combination of summer dormancy with cool winters, and fewer instars in the emerging cohort result in a shorter emergence period, with two modal groups that remain constant in size from year to year.

Females emerge slightly earlier during the year than males but, by the end of the emergence period, males predominate in the sex ratio.

5.4. *AUSTROLESTES COLENSONIS*

5.4.1. Diel Pattern of Emergence

5.4.1.1. Results Observations on the diel pattern of emergence of *A. colensonis* were made simultaneously with those described for *X. zealandica* in section 5.3.1.. Only a few individuals

of *A. colensonis* were found during the diel preiodicity studies but all of these emerged after sunrise (see Figs. 23 & 24 for time references).

On 24 January 1977 at Lake Sarah - 1s one final-instar larva in late metamorphosis was observed actively searching for an emergence site at 4:05 (sunrise 4:38). The larva left the water at 5:00 but returned again by 5:45. Later, by 9:45, it emerged and left the area by 10:45. On the same day another individual was seen to emerge at 16:45.

On 9 February 1978 at Isaac's Pond one *A. colensonis* emerged between 10:15 and 11:15 and a second individual emerged between the collection at 12:15 and the next collection at 16:15.

5.4.1.2. Comments The few observations made on the diel pattern of emergence of *A. colensonis* are insufficient to describe this pattern accurately. During regular exuviae collections made to determine the seasonal pattern of emergence, only a few individuals were found emerging after solar noon. The limited results may indicate that the diel emergence pattern of *A. colensonis* is similar to that observed for *X. zealandica*, *i.e.* daylight emergence and most of the daily emergence completed before solar noon. If so, then the regular collections of exuviae had a slight effect only, on the progress of emergence.

5.4.2. Seasonal Pattern of Emergence

5.4.2.1. Results The general pattern of emergence of *A. colensonis* (Figs. 34 to 36) shows emergence to take place in two distinct pulses. The first group emerges early during the emergence period and is separated from the second group by a period during which the rate of emergence is reduced. The second group emerges late during the emergence period and characteristically has a high rate of emergence for a relatively short period. Usually more than two-thirds of the annual emergence group appears during this latter period (Table 13) indicating that peak emergence is synchronised with the end of the emergence period.

Emergence began by widely differing dates from site to site, but the end of emergence was similar. The EM dates (Fig. 37, Table 12) were usually similar from year to year at a given site. The dates of $EM_{0,\ 10}$ and $_{50}$ varied from site to site, whereas those of EM_{90} and $_{100}$

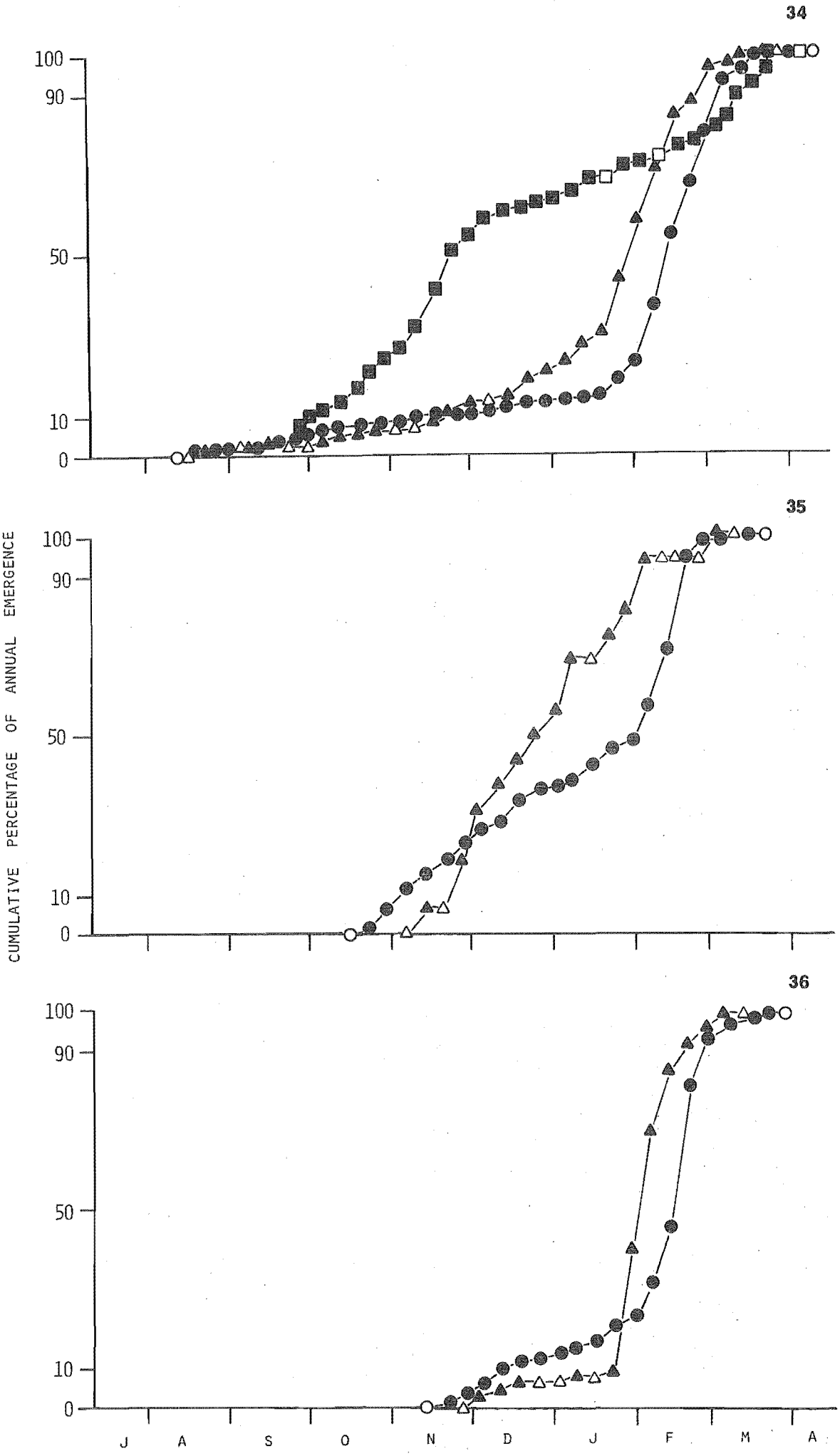
Fig. 34. Cumulative percentage of *Austrolestes colensonis* emerged at Isaac's Pond during 1975-1978.

Fig. 35. Cumulative percentage of *Austrolestes colensonis* emerged at Lake Sarah - tb during 1976-1978.

Fig. 36. Cumulative percentage of *Austrolestes colensonis* emerged at Lake Sarah - ls during 1976-1978.

List of symbols for Figs. 34 to 36.

Hollow symbol	-	no exuviae found
square	-	1975-1976
circle	-	1976-1977
triangle	-	1977-1978


34
35
36
100
90
50
10
0
CUMULATIVE PERCENTAGE OF ANNUAL EMERGENCE
J
A
S
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M
A

TABLE 12 SUMMARY OF EMERGENCE RESULTS FOR *AUSTROLESTES COLENSONIS*

Study Site	Emergence Period	Number of Exuviae	Dates of Specified EM Points EM_0	EM_{10}	EM_{50}	EM_{90}	EM_{100}	Duration of Emergence (Days)	Combined Range of EM_0 and EM_{100} (Days)	Mean Water Temperature (°C) at EM_0
	1975-1976	123	In Progress 28 Sept	1 Oct	24 Nov	12 Mar	26-28 Mar	>181	-	-
			(Approximations)							
Isaac's Pond	1976-1977	215	13-19 Aug	2 Dec	14 Feb	6 Mar	23-30 Mar	229	13	11 1/2
	1977-1978	116	17-24 Aug	23 Nov	31 Jan	23 Feb	17-24 Mar	219	14	10
	1978-1979		No emergence by 30 August							
Lake Sarah - tb	1976-1977	298	16-24 Oct	7 Nov	31 Jan	21 Feb	6-16 Mar	151	18	10
	1977-1978	16	6-14 Nov	17 Nov	26 Dec	7 Feb	26 Feb -5 Mar	119	15	11 1/2
Lake Sarah - ls	1976-1977	212	14-22 Nov	16 Dec	14 Feb	24 Feb	16-20 Mar	126	12	-
	1977-1978	64	27 Nov -3 Dec	17 Jan	30 Jan	17 Feb	26 Feb -5 Mar	96	13	15

Fig. 37. Cumulative emergence lines of *Austrolestes colensonis*. For sample size see Table 12. Hollow circles indicate the range in the start and end of emergence (see text).

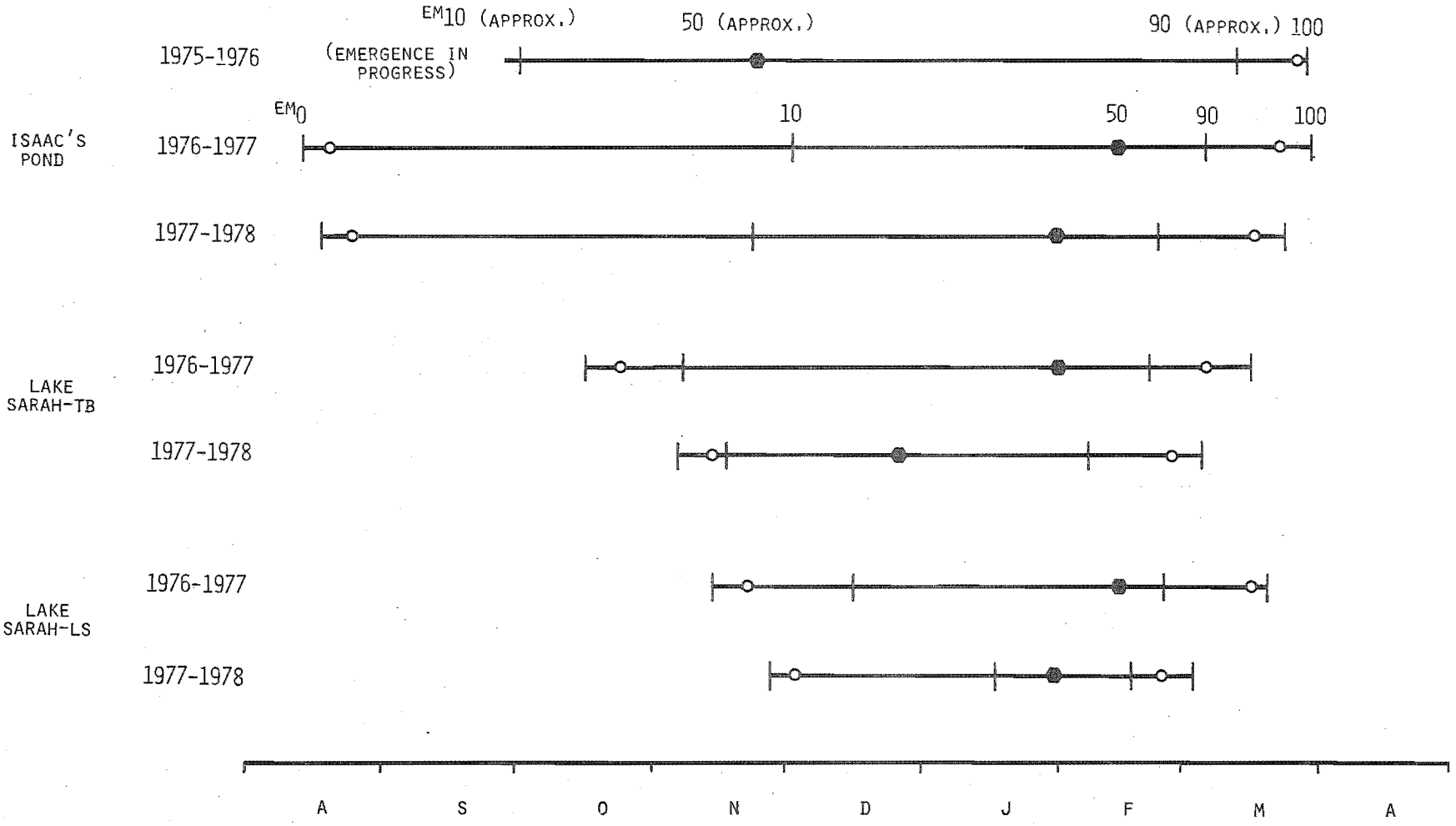

EM10 (APPROX.)
50 (APPROX.)
90 (APPROX.) 100
1975-1976
(EMERGENCE IN PROGRESS)
EM0
10
50
90
100
ISAAC'S POND
1976-1977
1977-1978
1976-1977
LAKE SARAH-TB
1977-1978
1976-1977
LAKE SARAH-LS
1977-1978
A
S
O
N
D
J
F
M
A

Fig. 38. Cumulative percentage of *Austrolestes colensonis* emerged at Lake Sarah - 1s, 1976-1977 (Abscissa on probability scale), n = 212.

List of symbols:

hollow - original distribution

solid - derived modes.

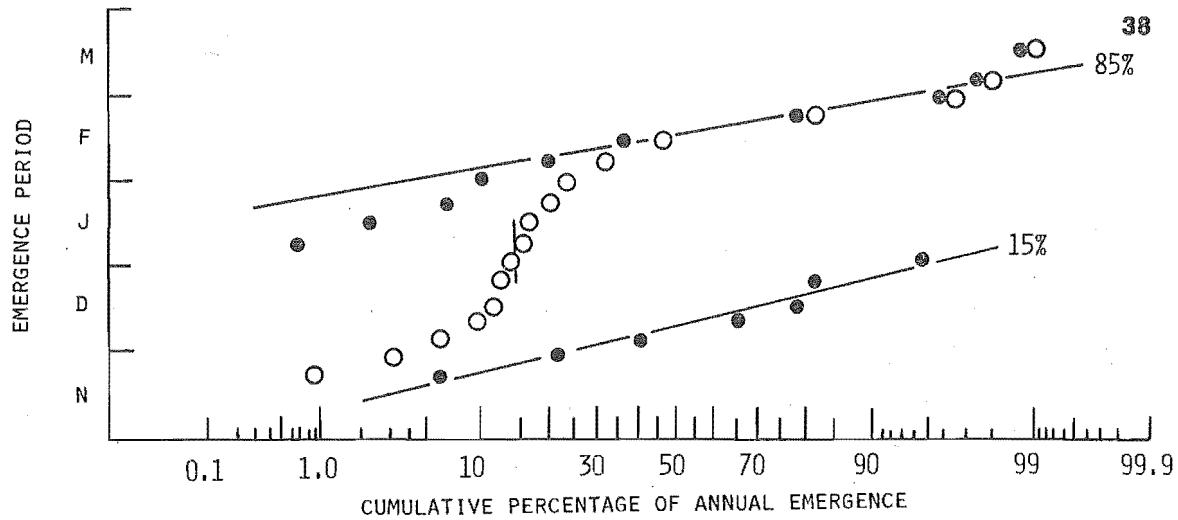
Fig. 39. Cumulative percentage of *Austrolestes colensonis* males emerged during annual emergence at Issac's Pond (1976-1977 and 1977-1978).

Fig. 40. Cumulative percentage of *Austrolestes colensonis* males emerged during annual emergence at Lake Sarah - 1s (1976-1977 and 1977-1978).

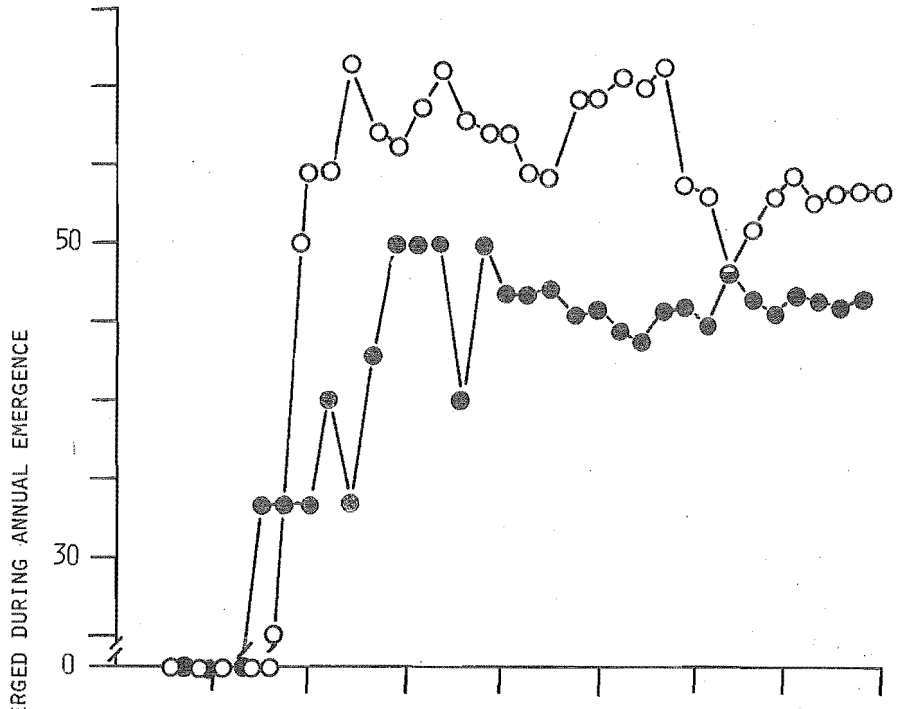
List of symbols for Figs. 39 & 40

- hollow symbols 1976-1977
- solid symbols 1977-1978

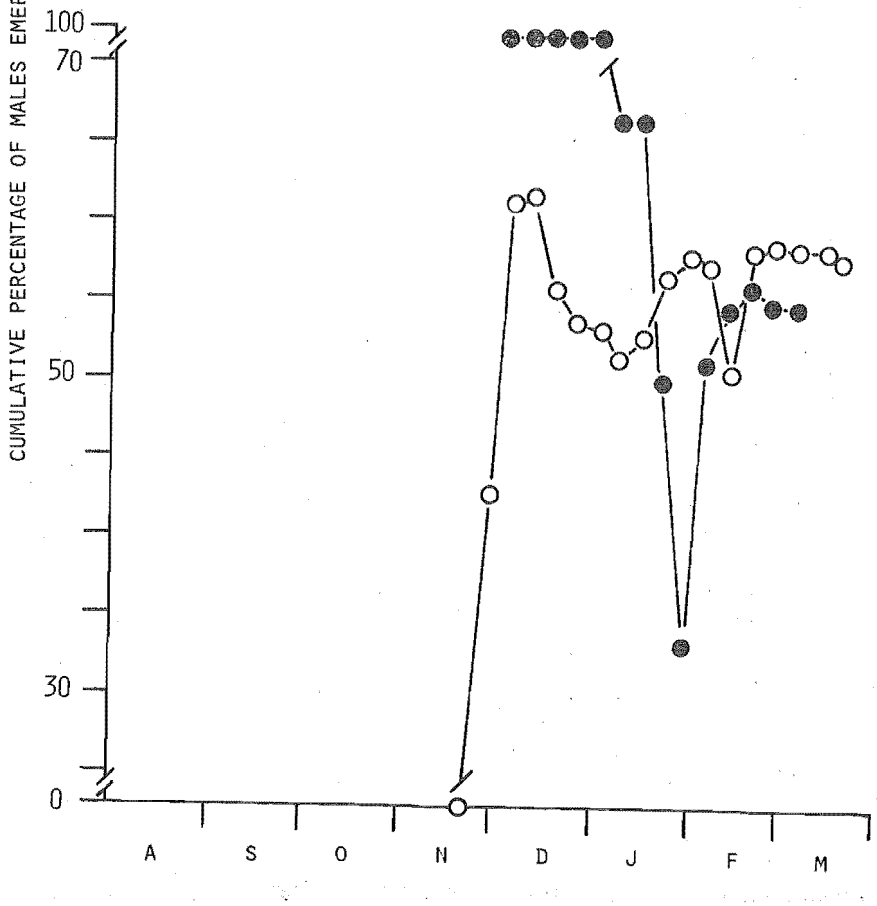
38


M
F
J
D
N
EMERGENCE PERIOD
85%
15%
0.1
1.0
10
30
50
70
90
99
99.9
CUMULATIVE PERCENTAGE OF ANNUAL EMERGENCE

39


50
30
0

40


CUMULATIVE PERCENTAGE OF MALES EMERGED DURING ANNUAL EMERGENCE
100
70
50
30
0
A
S
O
N
D
J
F
M

were similar.

The date of EM_0 was not observed at Isaac's Pond in 1975; therefore; the approximate dates of $EM_{10, 50}$ and $_{90}$ were calculated as described for *X. zealandica* (section 5.3.2.1.).

The mean water temperature for the week during which emergence started (Table 12) ranged from 10 to 11 1/2°C at all the sites, except at Lake Sarah - 1s during 1977 - 1978 when the mean water temperature was 15°C.

During the 'off-season' no emergence of *A. colensonis* was noted at any of the sites.

The total number of exuviae collected varied considerably from year to year at each site, especially at Lake Sarah - tb (Table 12). The number collected was substantially higher during 1976-1977 at all the sites.

Polymodality analyses consistently showed the emergence pattern of *A. colensonis* to be bimodal at all the sites (*e.g.* Fig. 38). Table 13 presents the calculated dates of Em_{50} of each mode and the percentage of the total annual population that each mode composed. The first mode is the smaller of the two, except at Isaac's Pond during 1975-1976 and at Lake Sarah - tb during 1977-1978.

TABLE 13. Modality of emergence of *Austrolestes colensonis*.

		MODE 1		MODE 2	
		Date EM_{50}	Percent of Annual Population	Date EM_{50}	Percent of Annual Population
Isaac's Pond	1975-1976	9 Nov	68	3 Mar	32
	1976-1977	6 Oct	10	18 Feb	90
	1977-1978	9 Nov	17	4 Feb	83
Lake Sarah - tb	1976-1977	15 Nov	31	9 Feb	69
	1977-1978	4 Dec	63	28 Jan	37
Lake Sarah - 1s	1976-1977	10 Dec	15	14 Feb	85
	1977-1978	5 Dec	7	4 Feb	93

5.4.2.2. Comments Unlike results obtained for *X. zealandica* at Isaac's Pond during 1975-1976 (section 5.3.1.2.) the approximations of the EM dates for *A. colensonis* at Isaac's Pond during the same period differed markedly from results for subsequent years (Table 12), as did the emergence pattern (Fig. 34). However, as noted for *X. zealandica*, the results for the following years indicated that only a small percentage of the total annual population of *A. colensonis* emerged before the end of September, about 3.7% and 2.6% in 1976-1977 and 1977-1978, respectively. Therefore, a similar accuracy in the approximations of the EM dates was expected for *A. colensonis* as was obtained for *X. zealandica*. Further, the low loss of *A. colensonis* exuviae was expected to have only a slight effect on the seasonal pattern of emergence.

At Isaac's Pond during 1975-1976 the exuviae collection site dried out during the late summer. This did not directly affect the larvae destined to emerge that season but it may have altered their behaviour. *A. colensonis* larvae actively search for a suitable emergence site (section 5.4.1.1.). The dried out collection site probably was unsuitable for emergence by late summer. Therefore, most of the remaining population emerged elsewhere, thereby producing the observed pattern of emergence (1975-1976, Fig. 34).

A similar pattern of emergence was observed at Lake Sarah - tb during 1977-1978 when the water level fell (section 3.3.4.2.). Parts of this site dried out, thereby affecting the population directly. As the water level decreased the larvae destined to emerge that season either died or moved away from the area. The water reached low levels during January and especially February which reduced the numbers in the second emergence group. This is substantiated by the low number of exuviae collected at Lake Sarah - tb during 1977-1978 (n = 16) as compared with that of 1976-1977 (n = 298) (Table 12).

The start of emergence was probably dependent on the same factors as described previously for *X. zealandica* (section 5.3.2.2.) Again rising water temperature is unlikely to limit the start of emergence. Emergence of *A. colensonis* started about 100 days earlier at Isaac's Pond, with its warmer 'off-season' water temperature regimen, than at the Lake Sarah sites.

The site to site variation of EM dates decreased through the emergence period. The least variation was shown in the dates of EM_{90} and $_{100}$ (Table 12). This, combined with peak emergence synchronised

with the end of theemergence period, indicated a growth restriction in the life history. An examination of larval results (section 4.4.1.) showed several factors that potentially affected emergence.

Some eggs hatch the summer that they are laid and some hatch the following spring, possibly in response to rising temperatures. This results in a split cohort. The larvae grow rapidly during the subsequent summer until they reach approximately the F-2 instar when a growth restriction prolongs development in that stage. The earlier instar larvae continue to grow; therefore, concentrating the cohort into a narrower range of instars. The larvae that moult into the F-2 or possibly later instars by a certain critical date make up the first mode of emergence and the rest of the larvae make up the second mode (see also p. 88).

The growth restriction in the F-2 and/or earlier instar larvae at Lake Sarah - tb occurred when water temperature and food were not limiting growth. As was the case for *X. zealandica* (section 5.3.2.2.), these factors indicate a dormancy period, probably diapause, that occurs in the F-2 and/or earlier instar larvae. This dormancy prevented moulting into the F-1 instar during January to April at Lake Sarah - tb. With no recruitment into the later instars emergence ended by March. Emergence also ended by March at Isaac's Pond indicating a similar timing of dormancy at that site. The agent inducing dormancy was probably photoperiod.

The variation in the number of exuviae collected at each site from year to year followed the same pattern as described for *X. zealandica* (section 5.3.2.2.). The maximum number of exuviae collected at Isaac's Pond was obtained during the second year of study, 1976-1977 (Table 12). This supports the conclusion that the number of exuviae collected was not related to collecting techniques but was probably a normal component of the population dynamics of the species. The small number of exuviae collected at Lake Sarah - tb during 1977-1978 was probably related to the decrease in water level and the effect that this had on emergence as explained earlier in this section.

At Isaac's Pond mild winter conditions resulted in an early start of emergence, as discussed earlier, and a long emergence period, whereas at Lake Sarah cool winters resulted in a later start of emergence and a shorter emergence period. However, a bimodal pattern of emergence was obtained at all three sites (Table 13). This is unlike the emergence pattern of *X. zealandica* (section 5.3.2.2.) which

was trimodal at Isaac's Pond but bimodal at the Lake Sarah sites.

As mentioned earlier in this section bimodal emergence probably resulted from a dormancy in the F-2 or earlier instars of *A. colensonis*. It was proposed that the first modal group was made up of larvae that reached the later instars by a certain critical date and that the second modal group consisted of the remainder of the cohort. A larval study on *A. colensonis* was carried out only at Lake Sarah - tb; therefore, it was possible to make only one comparison of the instar composition of the emerging cohort with the modal groups in the emergence period (see cohort 1, 1976, Fig. 19 and Lake Sarah - tb, 1976-1977, Table 13 respectively).

The best fit between instar composition and modality of emergence was obtained in the September 1976 sample. At that time the F and F-1 instar larvae made up 29.3% of the cohort. The first mode of emergence of that cohort contained 31% of the emerging population. The following month, at the start of emergence, the F and F-1 instar larvae made up 63% of the cohort. This may indicate that the emergence groups are determined by September at Lake Sarah. Because this is derived from one observation this conclusion must be treated with reserve.

The date of EM_{50} (Table 13) of the first modal group varied considerably; therefore, emergence was probably cued by temperature. However, the date of EM_{50} of the second modal group was similar at all the sites, except for Isaac's Pond 1975-1976 and Lake Sarah - tb 1977-1978. As mentioned earlier these latter two observations also showed unusual emergence patterns that were believed to be related to the low water levels recorded at these sites during the emergence period (see p. 86). From the remaining records EM_{50} occurred between 4 and 18 February. The temperature regimen differed markedly from site to site and year to year; therefore, emergence of this group was probably cued by photoperiod. The only evidence in support of this is the apparent accumulation of larvae in the F instar in cohort 1, December 1976 (Fig. 19); however, this is inconclusive because of the error involved in a small sample (n = 14). The possibility of a growth restriction regulating the emergence of the second modal group is examined further in the laboratory study (section 7.4.).

5.4.3. Sex Ratio

5.4.3.1. Results The sex ratio and pattern of appearance of the sexes was determined at the same sites and during the same years; Isaac's Pond and Lake Sarah - 1s during 1976-1977 and 1977-1978, as was the case for *X. zealandica* (for reasoning see section 5.3.3.1.).

Table 14 presents the sex ratios that were obtained for *A. colensonis* based on the complete emergence period. These show male excess to be slight and repeated in three of the four observations. Figures 39 & 40 show the changing proportion of males in the population during the emergence period. Males usually predominated shortly after the start of emergence. During peak emergence in late January to early February (see Figs. 34 & 36) a predominance of females was noted for a short time but by the end of emergence males again predominated.

TABLE 14. Sex ratios of *Austrolestes colensonis* based on collections of exuviae at Isaac's Pond and Lake Sarah - 1s during 1976-1977 and 1977-1978.

		Total Number Collected	Number Unsexed	Number of Males	Percent Males
Isaac's Pond	1976-1977	215	5	112	53.3
	1977-1978	116	2	53	46.5
Lake Sarah - 1s	1976-1977	212	1	122	57.8
	1977-1978	64	2	34	54.8

5.4.3.2. Comments These observations add to the literature four sex ratio records for one species. The records were based on exhaustive collections of exuviae made throughout the entire emergence period. As previously discussed for *X. zealandica* (section 5.3.3.2.), these results indicate that male predominance in the sex ratio may prevail in the Zygoptera.

Observations on the pattern of appearance of the sexes within the emergence period made by Fernet & Pilon (1971) indicated that males emerged earlier than females in *Lestes disjunctus* Selys. Ingram (1976b) also noted this pattern in *Lestes vigilax* Hagen. A similar trend occurred in *A. colensonis*; therefore, this pattern may be a characteristic of the Lestidae. As mentioned earlier (section 5.3.3.2.), the opposite pattern was observed in the Coenagrionidae; females emerged earlier than males.

The cause of this changing proportion of sexes of *A. colensonis* during the emergence period, or of an excess of one sex is unknown.

5.4.4. Summary

A. colensonis emerges after sunrise, probably with the majority emerging before solar noon.

The start of seasonal emergence is dependent on temperatures experienced during the winter and spring, not on a thermal threshold. Peak emergence is synchronised with the end of the emergence period. This is in part the result of a synchronous egg hatch followed by a summer dormancy in the F-2 (or earlier) instar larvae.

At Isaac's Pond mild winter conditions result in a long emergence period, whereas at Lake Sarah cool winters result in a shorter emergence period. The emergence pattern is bimodal at all the sites. The timing of emergence of the second mode is similar at all the sites which possibly indicates the existence of a mechanism in the emerging cohort that is cued by photoperiod and regulates emergence.

Males emerge slightly earlier during the year than females and males predominate in the sex ratio.

5.5. *PROCORDULIA SMITHII*

5.5.1. Diel Pattern of Emergence

During regular collections of exuviae, made to determine the seasonal pattern of emergence of *P. smithii* from Lake Sarah - tb, no emerging or teneral individuals were seen *in situ* or observed in their maiden flight from the emergence site. No study was made on the diel pattern of emergence of this species because of the difficulty

of making observations in the *Typha* - bed and because of the low incidence of emergence of this species (section 5.5.2.). Emergence may occur predominantly at night because no teneral individuals were seen during regular, daytime exuviae collections. However, the possibility that the species emerges after sunrise does exist. Prof. P.S. Corbet, Zoology Department, University of Canterbury, Christchurch (pers. comm. 1979) found an individual in the latter stages of emergence (wings fully expanded but pale cream coloured; abdomen in the process of expanding) at Lake Sarah - tb during the morning, about 4 1/2 to 5 1/2 hours after the start of Civil Twilight, on 4 January 1979. Regardless of the above the regular collections of exuviae probably had little, if any, effect on the emergence of this species.

5.5.2. Seasonal Pattern of Emergence

5.5.2.1. Results The exuviae of *P. smithii* were found only at the Lake Sarah - tb site and only in very low numbers during this study (Table 15). The patterns of emergence obtained are regarded as tentative only. They are presented with the results for *P. grayi* for ease of comparison.

The pattern of emergence during 1976-1977 (Fig. 41) showed emergence to take place in two distinct pulses. Peak emergence is synchronised with the end of the emergence period.

The first exuviae were collected two months later in 1977-1978 than in 1976-1977 (Table 15). Emergence during 1977-1978 occurred as a short burst (Figs. 41 & 44).

Polymodality analyses (Table 16) showed that emergence was bimodal in both seasons.

Fig. 41. Cumulative percentage of *Procordulia smithii* emerged at Lake Sarah - tb during 1976-1978.

Fig. 42. Cumulative percentage of *Procordulia grayi* emerged at Lake Sarah - ls during 1976-1978.

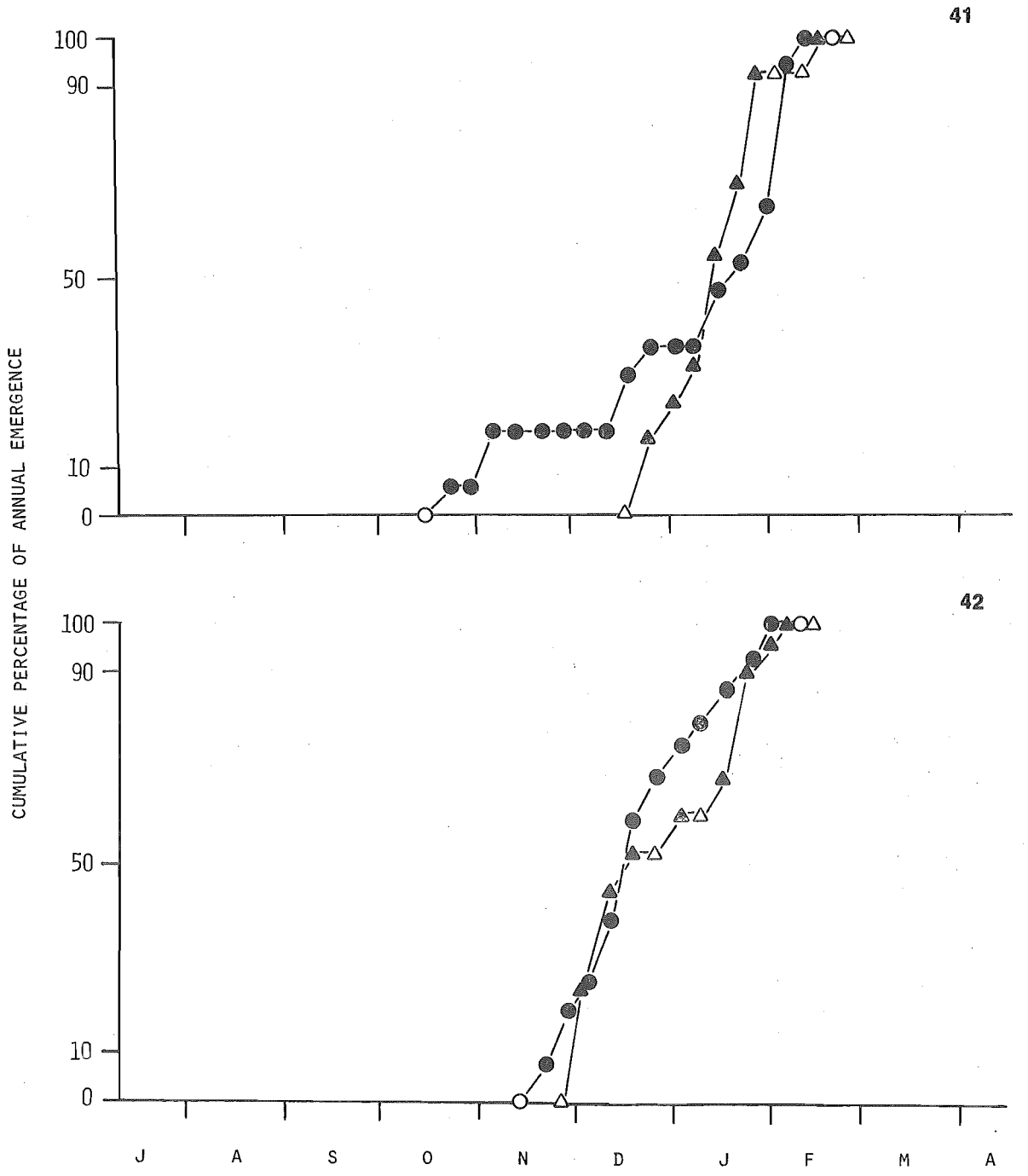
List of symbols for Figs. 41 & 42.

Hollow symbol	-	no exuviae found
circle	-	1976-1977
triangle	-	1977-1978

Fig. 43. Cumulative percentage of *Procordulia grayi* emerged at Lake Sarah - ls, 1976-1977 (Abscissa on probability scale); n = 120.

List of symbols:

hollow	-	original distribution
solid	-	derived modes.


41
42
100
90
50
10
0
CUMULATIVE PERCENTAGE OF ANNUAL EMERGENCE
J
A
S
O
N
D
J
F
M
A

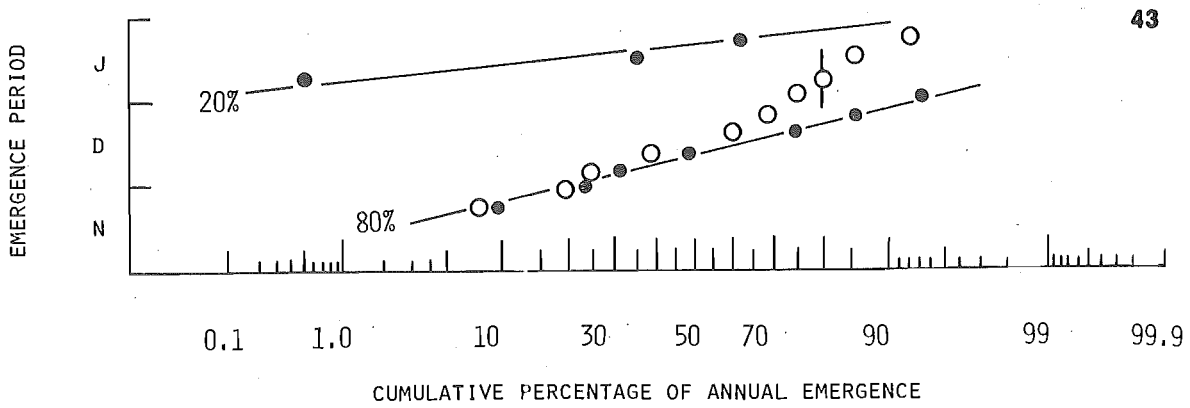

43
EMERGENCE PERIOD
J
D
N
20%
80%
0.1
1.0
10
30
50
70
90
99
99.9
CUMULATIVE PERCENTAGE OF ANNUAL EMERGENCE

TABLE 15 SUMMARY OF EMERGENCE RESULTS FOR *PROCORDULIA SMITHII* AND *PROCORDULIA GRAYI*

Species and Study Site	Emergence Period	Number of Exuviae	Dates of Specified EM Points EM_0	EM_{10}	EM_{50}	EM_{90}	EM_{100}	Duration of Emergence (Days)	Combined Range of EM_0 and EM_{100} (Days)	Mean Water Temperature (°C) at EM_0
Procordulia smithii	1976-1977	17	16-24 Oct	2 Nov	20 Jan	5 Feb	6-13 Feb	120	15	10
Lake Sarah - tb	1977-1978	13	18-25 Dec	24 Dec	15 Jan	2 Feb	12-19 Feb	63	14	14 1/2
Procordulia grayi	1976-1977	120	14-22 Nov	24 Nov	16 Dec	29 Jan	23-31 Jan	78	16	-
Lake Sarah - ls	1977-1978	25	27 Nov -3 Dec	29 Nov	16 Dec.	30 Jan	29 Jan -5 Feb	70	13	15

Fig. 44. Cumulative emergence lines of *Procordulia smithii* and *Procordulia grayi*. For sample size see Table 15. Hollow circles indicate the range in the start and end of emergence (see text).

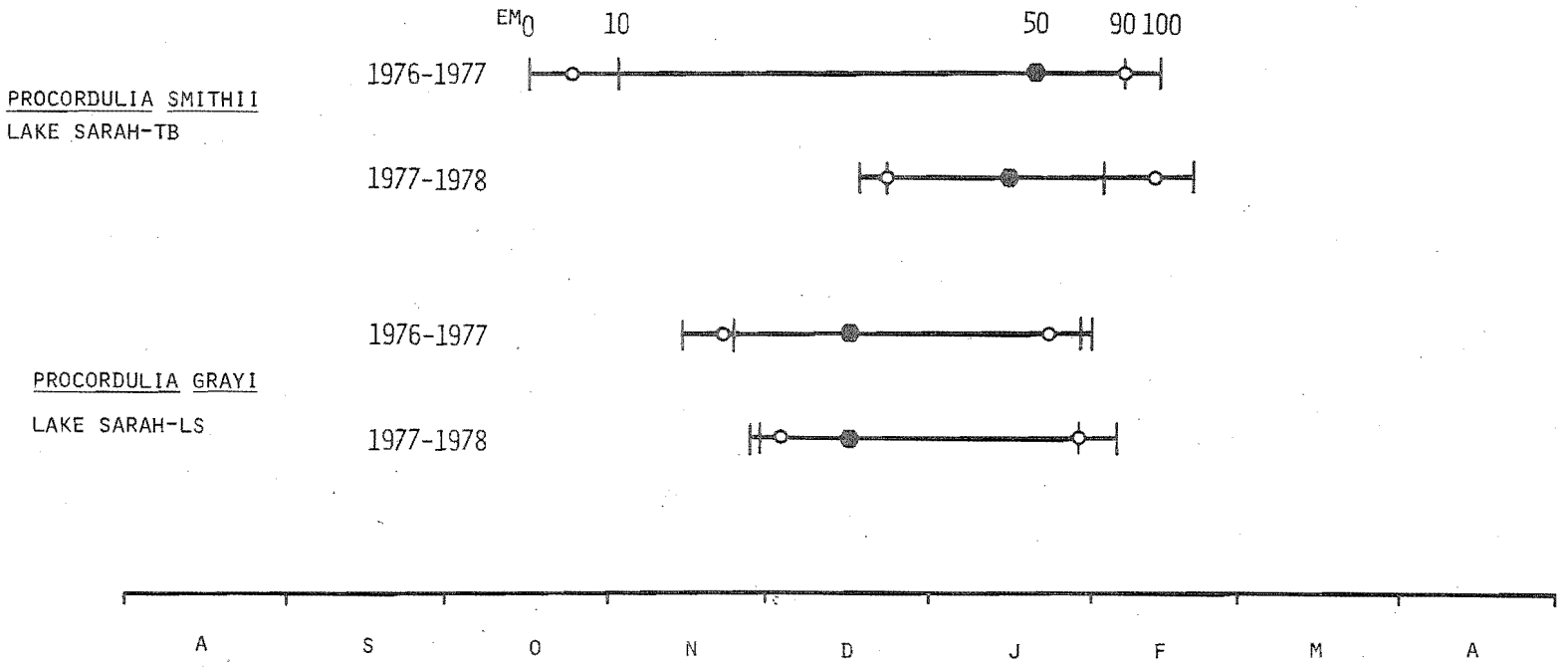

EM 0
10
50
90 100
1976-1977
PROCORDULIA SMITHII
LAKE SARAH-TB
1977-1978
1976-1977
PROCORDULIA GRAYI
LAKE SARAH-LS
1977-1978
A
S
O
N
D
J
F
M
A

TABLE 16. Modality of emergence of *Procordulia smithii* and *Procordulia grayi*.

		MODE 1		MODE 2	
		Date of EM_{50}	Percent of Annual Population	Date of EM_{50}	Percent of Annual Population
Procordulia smithii	1976-1977	20 Dec	59	3 Feb	41
Lake Sarah - tb	1977-1978	8 Jan	62	28 Jan	38
Procordulia grayi	1976-1977	10 Dec	80	21 Jan	20
Lake Sarah - ls	1977-1978	10 Dec	80	19 Jan	20

5.5.2.2. Comments The late start of emergence indicated by the exuviae collections in 1977-1978 was believed to be an artifact resulting from the small size of the sample. Emergence apparently started before 25 December 1977 (Table 15). Reproductively active adults were observed in the area before the first exuvia was collected indicating that emergence had started before 25 December. Alternatively, the adults could have emerged in a different area and moved to the Lake Sarah - tb site. However, the former suggestion is considered to be the most likely alternative. Apparently most of the first emergence group went undetected during 1977-1978 (Fig. 41). Consequently the modality obtained for the 1977-1978 emergence (Table 16) was probably erroneous too!

The emergence pattern obtained during 1976-1977 was considered to be characteristic for *P. smithii*. This was similar to the pattern obtained for *A. colensonis* (section 5.4.2.), with peak emergence synchronised with the end of the emergence period. The dates of EM_0 and $_{100}$ were also similar to those obtained for *A. colensonis* at Lake Sarah - tb during 1976-1977.

No attempt to correlate environmental factors with the pattern of emergence is made here because only one observation on *P. smithii* is available for comment. The similarity between the emergence patterns of *A. colensonis* and *P. smithii* may indicate that environmental factors affect both species in a similar manner.

The emerging cohort of *P. smithii* was made up of F and F-1 instar larvae at the start of emergence (p. 59) which possibly gave rise to the bimodal emergence pattern observed. A detailed comparison of the instar composition of the emerging cohort with the modal groups in the emergence period was considered unjustified because of the small sample sizes obtained in this study.

Peak emergence synchronised with the end of the emergence period possibly indicates a growth restriction, cued by photoperiod, that regulates the emergence of the second modal group. This is examined further in the laboratory study (section 7.5.).

5.5.3. Sex Ratio

No sex ratio information is available for this species. Characteristics could not be found to allow the positive determination of the sexes of the exuviae.

5.5.4. Summary

P. smithii possibly emerges before sunrise, or during the morning before solar noon.

The seasonal pattern of emergence is similar to that of *A. colensonis*. Environmental factors may affect the emergence of both species in a similar manner. Peak emergence is synchronised with the end of the emergence period.

Two modes of emergence occur. The timing of emergence of the second mode possibly indicates the existence of a mechanism in the emerging cohort that is cued by photoperiod and regulates emergence.

No sex ratio information is available.

5.6. *PROCORDULIA GRAYI*

5.6.1. Diel Pattern of Emergence

5.6.1.1. Results Although final instar larvae of *P. grayi* are relatively large and therefore, easily observed, they were not seen emerging from the Lake Sarah - ls site during regular collections of exuviae made to determine the seasonal pattern of emergence. On 24 January 1977 at Lake Sarah - ls, during the *X. zealandica* and

A. colensonis diel pattern of emergence study, observations were also made on *P. grayi*. A strip, 1.0m wide, along 70.0m of the shore was cleared of *P. grayi* exuviae by 15:15 on 23 January. (See Fig. 23 for time reference). No individuals had emerged by the check made at sunset. When this area was checked at 2:45 (start of Civil Twilight 4:05; sunrise 4:38) the next day, eight individuals were found, all with their wings fully expanded but held closed over the thorax. The air temperature was 12°C; there was no wind and there was 10 to 20% cloud cover. By the next check at 3:45 all the individuals had opened their wings and when checked at 4:05, all the tenerals had left their emergence sites. The air temperature had decreased to 9 1/2 to 10°C by this time (Fig. 23) and there was about 20% cloud cover.

On 7 January 1978, the same 70.0m strip was cleared of exuviae by 17:00 and checked again before sunset without additional exuviae being found. When the next check was made at 3:15 the following day (start of Civil Twilight 3:46, sunrise 4:21), five individuals were found all with their wings fully expanded but held closed over the thorax. An extremely strong 'North-Westerly' wind was blowing at this time and there was about 10% cloud cover. Two individuals opened their wings by 3:30, a third by 3:35 and the fourth by 4:00. The fifth individual was blown into the water between 4:00 and 4:15. The first individual left its emergence site by 3:35, two more individuals left by 3:50 and the last individual left by 4:15. The individual that was blown into the water crawled up a *T. orientalis* stem and did not leave the site until 10:45.

On 28 January 1978 the same area was cleared of exuviae before sunset. Checks were started the next day at 3:45 (start of Civil Twilight 4:11, sunrise 4:43). Only one individual was found, and then not until 4:40 by which time its wings were open. The air temperature was 12°C and there was no cloud cover. This specimen was collected and preserved before it could leave the site.

5.6.1.2. Comments The emergence of *P. grayi* appears to take place some time after sunset and well before sunrise as indicated by the stage in which teneral adults were found at the time of the earliest morning checks. The wings were expanded some time during the night and unless conditions were extreme (*e.g.*, strong winds) almost all the individuals opened their wings between 30 and 10 minutes of

the start of Civil Twilight, probably in response to increasing light intensity. Most individuals flew by the start of Civil Twilight, at an air temperature as low as 10°C and when cloud cover was low (approximately 10-20%), although if conditions were poor the maiden flight was postponed. The latest that an individual was seen to leave the emergence site was 10:45 Solar Time.

The daytime collection of exuviae of this species which emerges during the night had no effect on the progress of emergence.

5.6.2. Seasonal Pattern of Emergence

5.6.2.1. Results High numbers of *P. grayi* exuviae were found only at the Lake Sarah - ls site and only during 1976-1977 (n = 120, Table 15). During 1977-1978 25 exuviae were collected from the same site. No *P. grayi* exuviae were found at the Lake Sarah - tb site. Nine exuviae were found at the Isaac's Pond site during the three emergence periods from 1975 to 1978. To facilitate the presentation of the Isaac's Pond data each month during which emergence occurred was divided into three equal portions designated early, mid, and late. The total number of exuviae collected in each portion during 1975 to 1978 was then presented. Three individuals emerged in late October; two in mid-November; two in early December; one in late December; and one in late January.

The pattern of emergence at Lake Sarah - ls (Figs. 42 & 43) showed emergence to take place in two pulses. Peak emergence occurred during the first half of the emergence period. Emergence started slightly later in 1977-1978 than in 1976-1977 but ended by almost the same date both years (Fig. 44, Table 15).

Polymodality analyses showed the date of EM_{50} and the proportion that each modal group made up of the emerging population to be very similar each year (Table 16).

5.6.2.2. Comments The emergence pattern obtained during 1976-1977 (Fig. 42) was assumed to be reliable (n = 120) and therefore, considered to be characteristic for *P. grayi*. Peak emergence was apparently synchronised with the start of the emergence period (Figs. 42 & 44), the opposite of the situation found in *P. smithii* and different from the two zygopteran species.

The start of emergence, which occurred later in 1977-1978 than in 1976-1977, was probably related to temperature. However,

the end of emergence, which was similar in both years (Table 15), and which occurred while water temperature was not a factor limiting growth, was probably related to a growth restriction in the larvae that was cued to photoperiod (for reasoning see section 5.3.2.2., p. 75). Also, the identical modality results obtained for both years (Table 16) were an indication of some mechanism that acted independently of temperature to regulate emergence, *i.e.* photoperiod.

The few observations at Isaac's Pond showed a pattern of emergence similar to that observed at Lake Sarah - ls. Peak emergence occurred in late October to mid-November and emergence ended by late January. This perhaps indicates a similarity of emergence from sites known to experience a difference in temperature regimen and therefore, supports further the proposal that emergence is regulated by photoperiod.

If the above reasoning is valid then a growth restriction (dormancy), probably diapause, occurs in the larvae. No information on the growth pattern of the larvae of *P. grayi* is available at present. The above speculation about a growth restriction in *P. grayi* must remain unconfirmed until information concerning larval growth and development becomes available.

5.6.3. Sex Ratio

No sex ratio information is available for this species. Characteristics could not be found to allow the positive determination of the sexes of the exuviae.

5.6.4. Summary

P. grayi emerges some time after sunset and flies by the start of Civil Twilight.

The seasonal pattern of emergence is dissimilar to that of the other three species in this study. The start of emergence is probably related to temperature. Peak emergence is synchronised with the start of the emergence period.

Two modes of emergence occur, both of which appear to be cued by photoperiod which indicates a growth restriction in the larvae. This remains unconfirmed at present.

No sex ratio information is available.

LABORATORY STUDY

The laboratory study was designed to provide details about the development of egg and larval stages that could not be determined from the field study. The results from the field study indicated the presence of possible growth restrictions in various life stages. The development of these life stages was examined under experimental conditions in the laboratory and the nature of the growth restriction (if any) was determined. After a growth restriction was identified an attempt was made to relate the responses observed in the field and the laboratory with environmental factors.

6. EGG STUDY

6.1. INTRODUCTION

The egg study was carried out for two reasons.

Firstly, it served as a check on the egg hatch results obtained from the field work. Almost all of the second and most of the third instar larvae passed through the netting used in sampling (section 4.2.2.). Therefore, the larval survey did not provide an exact means for determining the hatching period in the field. Some indication of hatching was obtained (sections 4.3., 4.4., & 4.5.), but usually only a few early instar larvae were collected in a sample. The results from the egg study provided the information needed to confirm or refute the inferences based on the field observations. No larval survey was carried out on *P. grayi*; therefore, the egg study provided the only information on the embryonic development of this species.

Secondly, the egg study examined the nature of the possible growth restriction in the eggs of *A. colensonis* and *P. smithii* that was indicated by the field work (sections 4.4. & 4.5.).

6.2. EXPERIMENTAL CONDITIONS

The same photoperiod and temperature conditions were used for experiments in both the egg and larval studies. The two photoperiod

regimens used were 16L:8D and 10L:14D, hereafter referred to as the LD (long day) and SD (short day) photoperiod, respectively. The photophase was centred around solar noon. See section 3.3.3. for further details about photoperiod. The automatic timers used to control the lights were accurate to within ± 2 min per 24 - hour cycle. Any deviations from these two photoperiods are indicated in the appropriate sections.

Several photoperiod and temperature combinations were used for various experiments. The intended conditions were:

- LD 25, 20, 17.5, 15, 12.5, 10, 7.5, & 6°C; and
- SD 20°C.

Except for 25°C, the temperatures were selected to represent the range of conditions normally experienced in the water at the study sites (see section 3.3.2.). The 25°C temperature was higher than the maximum water temperature recorded from the study sites, but was experienced in other ponds within the range of the species studied (see for example Barclay 1966; Crumpton 1978). The 7.5°C temperature represented winter conditions and the 6°C temperature was used in a special study on diapause (see section 6.6.2.).

Mercury bulb maximum-minimum thermometers, calibrated as described earlier (section 3.3.2.), provided daily temperature records from which the mean water temperatures were calculated for the duration of each experiment. Faulty equipment occasionally caused major deviations from the intended conditions, especially at 12.5 and 10°C. The thermostats, used to control these two temperatures, often allowed a daily fluctuation of ± 2 to 4°C. The recorded mean water temperature is presented in the subsequent sections.

The experiments were carried out in light proof, wooden cabinets, internal dimensions 0.8m long, 0.5m wide, and 0.6m high. A small fan provided ventilation and ensured that temperatures within the cabinets remained relatively independent of the artificial photoperiod. A 20 - watt 'Atlas - Artificial Daylight' fluorescent lamp provided illumination. The light intensity in the cabinets during the experiments varied from 10 to 230 lux depending on proximity to the light source. This is well above the level recorded at the start and end of morning and evening Civil Twilight, respectively (3.55 lux). This light intensity was considered to be sufficient to stimulate a photoperiodic response in the odonates studied (see section 3.3.3.).

The cabinets were housed at an ambient temperature that was lower than the required experimental conditions. The temperature in the cabinet was regulated by a thermostat controlling a heating unit.

Walk-in environmental chambers, internal dimensions 2.0m long, 1.5m wide, 2.4m high, were used for the LD20, 15 and 6°C conditions. The light intensity during the experiments was always between 10 and 250 lux and, because of better temperature regulatory equipment, the temperature fluctuations were usually less than ± 1°C per day.

6.3. METHODS AND ANALYSES

6.3.1. Egg Collection

Eggs from the *Procordulia* species were obtained from females collected in copula which allowed both sexes to be positively identified to species. Oviposition was induced in the field by repeatedly dipping the end of the abdomen into a clear, glass vial (internal diameter 25mm; height 75mm) containing water, for example, see Calvert (1929). Lifting the abdomen completely out of the water helped to wash off attached eggs and to stimulate continued oviposition. Eggs were kept in an insulated container at the ambient water temperature until they could be returned to the laboratory and set up in the experimental conditions.

Eggs from *X. zealandica* were also obtained from females collected in copula. Because eggs are laid endophytically, females were returned to the laboratory for oviposition. Their wings were clipped to prevent escape and they were placed in a white plastic tray, 6.5cm deep, containing eight petri plates each with a moistened piece of filter paper (Nr 595 Carl Schleicher & Schull). The filter papers were folded in half (twice) to form a wedge of one quarter the surface area of the original. The tray and contents were placed under one 20-watt fluorescent and two 25-watt incandescent lamps. This provided a high light intensity and a maximum air temperature of 37°C. The filter paper with eggs was replaced after four hours and the eggs were immediately set up in the experimental conditions and kept wet in about 5.0mm of water.

Eggs from *A. colensonis* were obtained in the same manner as described for *X. zealandica* except that fresh *T. orientalis* stems were

used for the oviposition substrate instead of moistened filter paper. The stems were placed in 5.0mm of water and replaced after four hours. The eggs were immediately set up in the experimental conditions. Sawchyn and Church (1973), working with various lestids in Canada, dissected the eggs out of the stems before setting them up; however, in the present experiments the stems were simply cut into pieces and the pieces distributed among the experimental conditions. Stem pieces were kept wet in about 5.0mm of water.

At Lake Sarah - tb *A. colensonis* eggs of an unknown age were obtained by collecting *T. orientalis* stems showing oviposition scars. Stems were collected in a search made throughout the *Typha* - bed, trimmed, and kept in a paper bag for transport to the laboratory. During the winter the stems were transported in a cooler, with freezer packs, to keep the eggs cold. From 30 July 1977 one third of the stems were preserved in Pempel's fluid immediately after collection. During the winter the preservative was kept at 0°C to avoid the possibility of stimulation of hatching by a sudden exposure of the eggs to an unseasonably high temperature.

6.3.2. Maintenance and Termination

The freshly laid eggs were placed in plastic petri plates, 9.0cm in diameter, with aged, oxygenated water at room temperature. These plates were set up in the various conditions and examined for hatching at 24 - hour intervals between approximately 15:00 and 16:00 each day. Larvae were removed at each check and a record kept of the number hatched. After the last hatch the daily examination of eggs was continued for two weeks, after which checks were made at weekly intervals until the experiment was terminated.

An experiment was terminated when all hatching was completed and the remaining eggs were clearly dead or undeveloped (infertile). The eggs were examined at 50 X magnification using a Wild M5 Dissecting Microscope. The freshly laid eggs of all the species were creamy-white. Within 48 hours the fertile eggs of the *Procordulia* species turned reddish-brown. Those of *X. zealandica* and *A. colensonis* turned greyish-white to amber, whereas the polar cap at the anterior end turned orange-brown. Undeveloped eggs remained creamy-white. A hatched egg, which often had the exuvia of the prolarva still attached, was recognised

by a split in the darkened chorion. A dead egg either showed signs of a decaying embryo or sometimes was blackened by fungi. After the breakdown of the yolk in dead and undeveloped eggs, they appeared granular because of an accumulation of large droplets of fat. Eggs that could not be classified were returned to the experimental conditions and re-examined at a later date.

Some freshly laid eggs were set up in the field in vials with an internal diameter of 25mm and a height of 75mm that were closed with netting of a mesh size with internal measurements of 0.26mm by 0.26mm; 0.34mm across the diagonal. The netting excluded predators, permitted gas diffusion, and retained freshly hatched larvae. The vials were examined for hatching at each subsequent visit to the site.

6.3.3. Analyses

For each species the percentage of the eggs hatched, dead and undeveloped was calculated and presented in tabular form along with the values for the total hatching period (days after oviposition or collection) and the incubation period by which 50% of the successful egg hatch took place (egg hatch 50%). Brittain (1977), in work on the stonefly *Taeniopteryx nebulosa* (L.), considered this method of calculating mean egg hatch (egg hatch 50%) to be a relevant estimate of the incubation period for the whole population of eggs. When more than one period of hatching occurred each of the values for the hatching period and egg hatch 50% were calculated.

For each species the relationship between hatching time (egg hatch 50%) and water temperature was usually well described by a hyperbola; therefore, there existed a linear relationship between rate of development (reciprocal of hatching time) and temperature. Elliott (1978), working on the eggs of the mayfly *Ephemerella ignita* (Poda), found that when such a relationship existed the time taken for development could be expressed in units of degree days above a threshold temperature. He calculated the linear regression line for the relationship between rate of development and temperature and from the equation for the line, he determined the number of degree days for development to be completed (^{1}/regression coefficient) and the threshold temperature (the temperature at which the developmental rate is zero). This same procedure was used here. For a full description and discussion of this method see Andrewartha & Birch (1954). The equation for the linear regression line is presented and the line shown on the graphs

(*e.g.*, see Fig. 45).

6.4. *XANTHOCNEMIS ZEALANDICA*

6.4.1. Rate of Development

6.4.1.1. Results The source of the eggs used in the experiments is indicated in Table 17. A single female collected at Lake Sarah, 16 December 1977, and one collected at Isaac's Pond, 9 February 1978, laid 87 and 199 eggs, respectively. The five females collected at Lake Sarah, 4 February 1978, and the eight females collected at Isaac's Pond, 10 February 1978, laid a total of 641 and 819 eggs, an average of 128 and 102 eggs per female, respectively.

Egg experiments at the conditions indicated (Table 17) were started on the date of collection. The developmental fate of the eggs and hatching periods are presented in Table 17. The linear regression line for the relationship between rate of development, when development occurred, and temperature was calculated using all the results except the field experiements (Table 17). From the equation for this line (Fig. 45) the number of degree days for development to be completed was 188.6 and the threshold temperature was 10.8°C.

6.4.1.2. Comments The number of eggs laid per female (87-192) is presented here as a record of the batch size of *X. zealandica*. The age, nutrition, past history, *etc.* of the female, and conditions in the laboratory probably influenced the values observed. Further observations on batch size and the number of batches produced per female are necessary before comment is possible on the reproductive potential of this species.

The eggs of *X. zealandica* developed directly within the temperature range from 24.5°C to 12.2°C, but as temperatures approached the threshold temperature (10.8°C) the hatching success decreased and the percentage of dead and undeveloped embryos increased (Table 17). Below the threshold temperature no hatching took place and as temperature decreased further, a greater percentage of eggs remained undeveloped. At 7.6°C (Table 17), almost all the eggs remained undeveloped and eventually died. This indicated that the calculated threshold temperature represented a real biological limit for the development of the eggs of *X. zealandica*.

TABLE 17. Egg study results for *Xanthocnemis zealandica*. Eggs incubated at LD photoperiod except for * SD photoperiod, and natural temperature and photoperiod at ** Isaac's Pond and + Lake Sarah. Source of eggs:

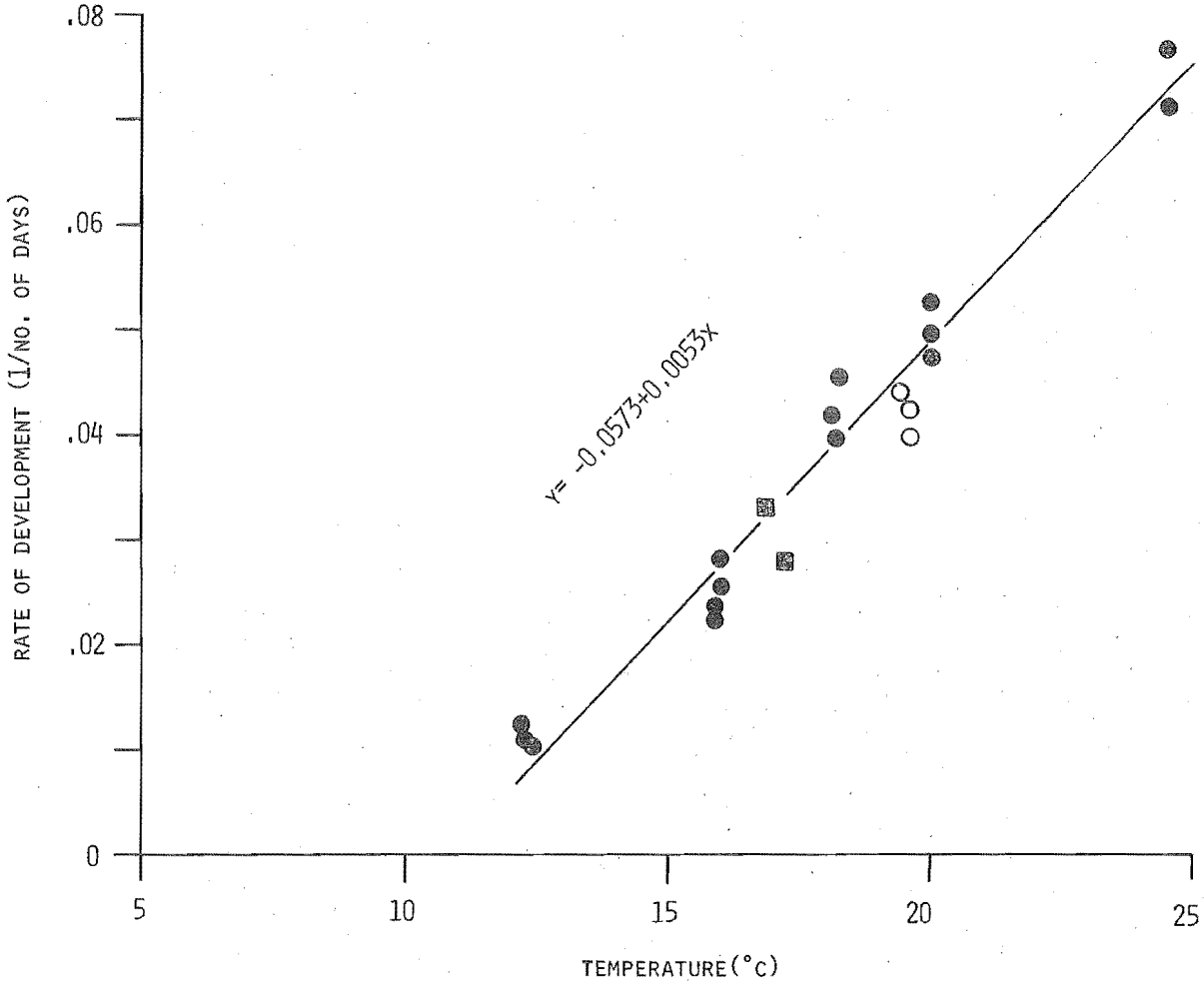
- 1 one female, Lake Sarah, 16 December 1977;
- 2 five females, Lake Sarah, 4 February 1978;
- 3 one female, Isaac's Pond, 9 February 1978; and
- 4 eight females, Isaac's Pond, 10 February 1978.

Source of Eggs	Temperature (°C) (mean and range)	Number of Eggs	Hatching Success (%)	Dead Embryos (%)	Undeveloped Eggs (%)	Hatching Period (days after oviposition)	Egg Hatch 50% (days)
2	24.5±2	89	93.2	3.4	3.4	14-16	14
3	24.5±2	21	95.2	0	4.8	13-16	13
4	24.5±2	76	90.8	1.3	7.9	12-16	13
1	20.0±1/2	25	100	0	0	21-22	21
2	20.0±1/2	106	91.5	0	8.5	19-22	20
3	20.0±1/2	23	100	0	0	19-20	19
4	20.0±1/2	90	95.6	2.2	2.2	18-20	19
2	19.6±2*	93	87.1	4.3	8.6	23-28	24
3	19.6±2*	32	100	0	0	23-24	24
4	19.4±1*	66	95.5	1.5	3.0	22-28	23
2	18.2±2	103	92.2	1.0	7.0	24-27	25
3	18.2±2	19	100	0	0	22-24	22
4	18.1±2	84	97.6	0	2.4	23-31	24
1	16.0±1	62	100	0	0	37-41	39
2	16.0±2	121	91.7	4.1	4.1	42-49	43
3	15.9±1 1/2	25	72.0	16.0	12.0	41-43	43
4	15.9±1 1/2	64	93.8	1.5	4.6	42-48	43
3	12.3±4	19	78.9	0	21.1	91-95	92
4	12.3±4	74	91.9	1.3	6.8	86-97	90
2	12.2±4	87	79.3	3.4	17.2	81-127	82
2	8.6±3	21	0	47.6	52.4	-	-
3	8.6±3	19	0	31.6	68.4	-	-
4	8.6±3	107	0	15.9	84.1	-	-
2	7.6±2	21	0	0	100	-	-
3	7.6±2	22	0	0	100	-	-
4	7.6±2	127	0	4.7	95.3	-	-
3	17.2±4**	12	100	0	0	36-38	36
4	16.9±4**	20	90	0	10	28-32	30
3	12.9±5+	7	0	0	100	-	-
4	12.9±5+	50	0	0	100	-	-

Fig. 45. Relationship between temperature and rate of development for egg hatch 50% of *Xanthocnemis zealandica*. The equation and calculated linear regression line are shown.

Symbols:

hollow circles	-	SD photoperiod
solid circles	-	LD photoperiod
solid square	-	natural photoperiod.


.08
.06
.04
.02
0
5
10
15
20
25
RATE OF DEVELOPMENT (1/NO. OF DAYS)
TEMPERATURE (°C)
Y= -0,0573+0,0053X

A comparison of the hatching period and egg hatch 50% (Table 17) of the individuals from Lake Sarah with those from Isaac's Pond showed the results from corresponding conditions to be similar. Initially the linear regression line was derived for each of the three replicates, indicated 2 to 4 in Table 17, and compared. These differed only slightly. For example, the maximum difference in threshold temperature, calculated from each of the equations was 0.4°C (10.5 to 10.9°C). The response of eggs collected either from Lake Sarah or Isaac's Pond was considered to be the same; therefore, all the results, excluding field experiments, were pooled to calculate the linear regression line (Fig. 45). The linear relationship between the two variables (rate of development of the eggs and temperature) was highly significant ($P<0.001$).

An examination of the results from the SD photoperiod group in each replicate showed the observed rates to fall within the 95% confidence limits calculated for each line. This indicated that the eggs did not respond differentially to the SD and LD photoperiod ($P>0.05$); therefore, the results for the SD photoperiod group were included when calculating the linear regression line.

The rate of development of the eggs set up in the field, at Isaac's Pond 9 February 1978, fell outside the 95% confidence limits calculated from the laboratory results for a mean temperature of 17.2°C. However, the rate of development of the group set up at Isaac's Pond on 10 February 1978, fell within the limits calculated for 16.9°C. Both the field experiments indicated direct development of the eggs under natural conditions. The 10 February group developed at a rate that did not differ significantly from the predicted value obtained from the laboratory results. Temperature appeared to be the major factor regulating the rate of development. The 9 February group developed at a slightly lower rate than expected, probably because of an accident during the experiment which exposed these eggs, for a period of up to seven days, to slightly cooler conditions than indicated by the temperature recorder. The eggs were set up near the temperature probe of the recorder, but the 9 February group was dislodged from this site and settled into a deeper, possibly cooler area of the channel.

Eggs that were set up in the field at Lake Sarah failed to develop (Table 17). Anaerobic conditions developed in the vials containing the eggs, shortly after the experiment was set up. The

area, in which the vials were located, experienced poor water circulation because of dense, emergent *T. orientalis*. Also, a fine silt clogged the netting that closed the vial. Both of these factors restricted the diffusion of gases from the vial which eventually resulted in the death of the eggs.

6.4.2. Summary

There was no evidence of diapause in the eggs of *X. zealandica* during this study. The laboratory and field experiments indicated direct development related to temperature. This confirmed that the eggs hatch the summer that they are laid, as observed during the field work. Prolonged incubation at 8.6°C or lower resulted in the death of all the eggs. This may apply up to the calculated threshold temperature of 10.8°C. If so, then the only hatch of eggs occurs before the onset of cold conditions at the end of summer. Any remaining eggs would die during the winter at both sites.

6.5. *AUSTROLESTES COLENSONIS*

6.5.1. Rate of Development

6.5.1.1. Results The eggs used in these experiments (Table 18) were obtained from nine females collected at Lake Sarah, 13 March 1978. The experimental conditions, the developmental fate of the eggs and the hatching periods are presented in Table 18. The linear regression line for the relationship between rate of development and temperature was calculated using all the results. From the equation for this line (Fig. 46) the number of degree days for development to be completed was 333.3 and the threshold temperature was 6.4°C.

6.5.1.2. Comments A total of 310 eggs were collected from the females in the laboratory. Because of a reluctance to lay eggs by some, and a strong tendency towards cannibalism by others, the exact number of females ovipositing was unknown. Therefore, no comment is possible on the number of eggs laid per female.

The eggs of *A. colensonis* developed directly within the temperature range examined (7.1 to 24.1°C) (Fig. 46, Table 18). The percentage of hatching was never as high as seen for *X. zealandica* (Table 17); the

TABLE 18. Egg study results for *Austrolestes colensonis*. Eggs incubated at LD photoperiod except for * SD photoperiod, and + natural temperature and photoperiod at Lake Sarah - tb.

Temperature (°C) (mean and range)	Number of Eggs	Hatching Success (%)	Dead Embryos (%)	Undeveloped Eggs (%)	Hatching Period (days after oviposition)	Egg Hatch 50% (days)
24.1±2	44	52.3	4.5	43.2	17-31	18
20.0±1	26	69.2	11.5	19.2	23-29	25
18.9±2*	31	54.8	16.1	29.0	27-36	28
18.0±1 1/2	27	70.4	0	29.6	27-31	29
15.8±1 1/2	47	61.7	0	38.3	43-46	44
11.5±4	43	55.8	9.3	34.9	73-136	75
8.3±2	36	44.4	5.5	50.0	163-185	164
7.1±1	20	30.0	5.0	65.0	214-235	215
12.0±5+	36	0	0	100	-	-

maximum success rate for *A. colensonis* was about 70% (Table 18). The percentage of the embryos that died showed no relationship with temperature; however, the percentage of undeveloped eggs increased with decreasing temperature (Table 18). A similar relationship between undeveloped eggs and low temperature was noted in *X. zealandica* (Table 17), especially below the threshold temperature. Although the threshold temperature differed by about 4°C between these two species, the eggs appeared to be affected by the cold in a similar manner. Temperatures near or below the threshold inhibit early embryonic development and eventually cause the death of the embryo.

The linear relationship between the rate of development of the eggs and water temperature was highly significant ($P<0.001$). The results from the SD photoperiod group fell within the 95% confidence limits for 18.9°C. This indicated that the eggs did not differ in response to the LD or the SD photoperiods. Temperature appeared to be the major factor regulating the rate of development.

Eggs that were set up in the field at Lake Sarah - tb failed to develop (Table 18). They were probably affected in the manner previously described for *X. zealandica* (section 6.4.1.2.) which resulted in the death of the eggs because of oxygen starvation.

Fig. 46. Relationship between temperature and rate of development for egg hatch 50% of *Austrolestes colensonis*. The equation and calculated linear regression line are shown.

Symbols:

hollow circles - SD photoperiod

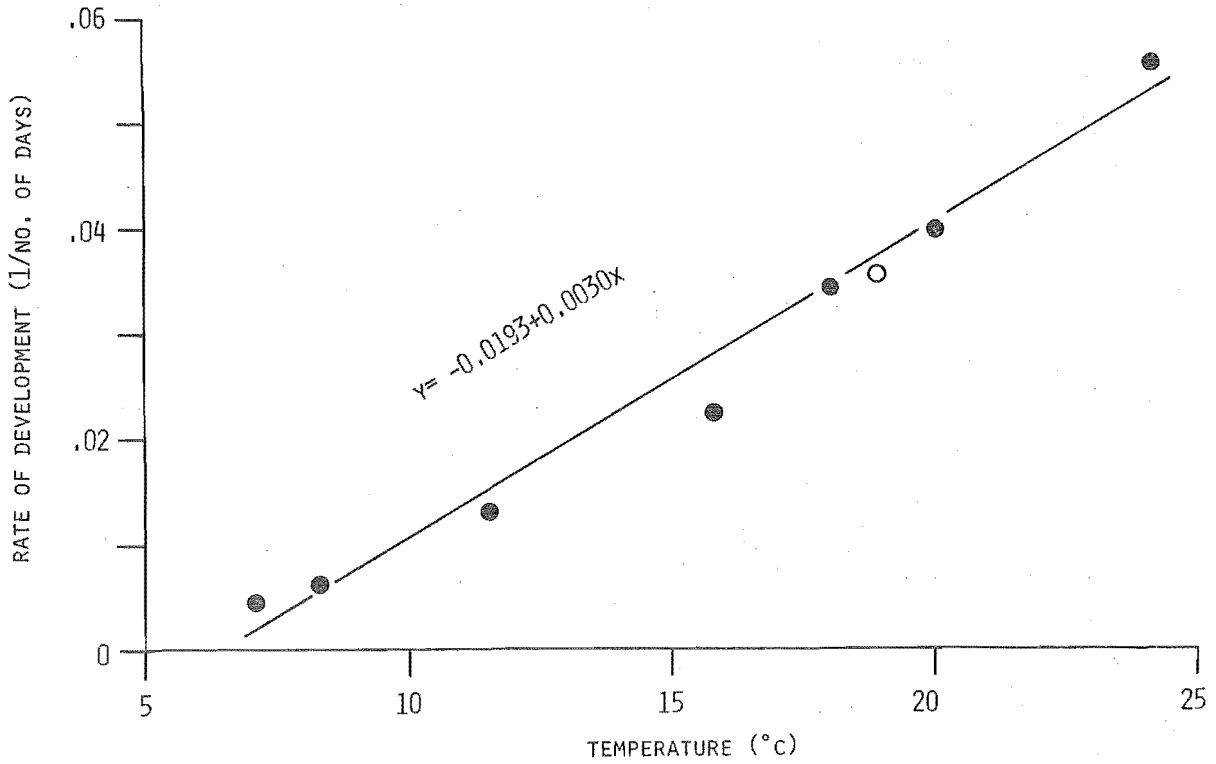
solid circles - LD photoperiod

Fig. 47. Incubation period in the laboratory of *Austrolestes colensonis* eggs collected in stems from Lake Sarah - tb during 1977. Egg hatch 50% and hatching period range calculated from combined photoperiod observations (LD & SD) at 20°C. Numbers above collection dates indicate:

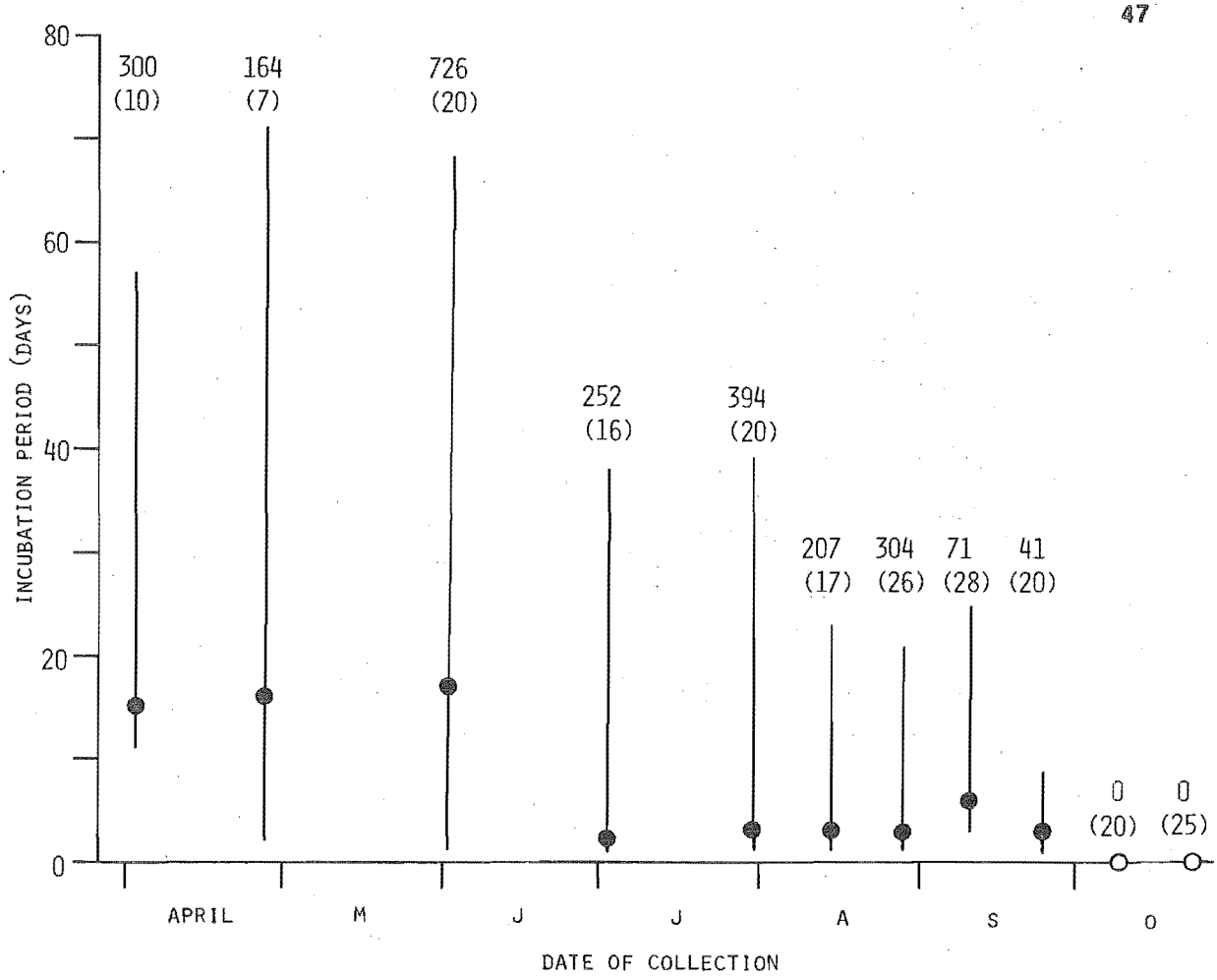
upper - eggs hatched;

lower - stems used in experiment.

46


.06
.04
.02
0
RATE OF DEVELOPMENT (1/NO. OF DAYS)
Y= -0.0193+0.0030x
5
10
15
20
25
TEMPERATURE (°C)

47


80
60
40
20
0
INCUBATION PERIOD (DAYS)
300 (10)
164 (7)
726 (20)
252 (16)
394 (20)
207 (17)
304 (26)
71 (28)
41 (20)
0 (20)
0 (25)
APRIL
M
J
J
A
S
O
DATE OF COLLECTION

There was no evidence of diapause in the eggs of *A. colensonis* in the above studies. The laboratory experiments indicated direct development, even at relatively low temperatures. This confirmed that the eggs can hatch the summer that they are laid, as observed during the field work.

6.5.2. Hatching Readiness

The field work at Lake Sarah - tb (section 4.4.1.) indicated that the eggs began to hatch the summer that they were laid but, because of the onset of cold weather or possibly a dormancy period, hatching was not completed until the following spring. Experiments were carried out in the laboratory during 1977-1978 to determine the developmental state of the eggs 'hatching readiness' collected in the field at various times during the summer and winter. The stems that were brought back to the laboratory were divided in half and set up at LD and SD 20°C conditions only. Egg hatch 50% and the hatching period from the time that the eggs were collected from the field was noted. The stems that were preserved in the field and later dissected in the laboratory were examined for the hatched, dead or developed, and undeveloped eggs. At least 200 eggs were dissected from a total of 10 stems on each occasion.

6.5.2.1. Results No difference in response between eggs set up in LD and SD photoperiods was evident. The combined results from the LD and SD conditions are presented in Fig. 47.

The range of the hatching period and the incubation period for egg hatch 50% decreased with progressively later collections. This was particularly noticeable between the collection of 1 June and that of 2 July. No eggs hatched from the stems collected on 9 and 23 October 1977.

6.5.2.2. Comments Results from section 6.5.1. indicated that freshly laid eggs of *A. colensonis* did not respond differentially to the LD and SD photoperiods. Eggs of various ages, collected from the field for the 'hatching readiness' experiments, responded to both photoperiods in the same manner. Therefore, it can be stated confidently that the eggs of *A. colensonis* do not respond differentially to the LD (16L:8D) and SD (10L:14D) photoperiods. This probably applies to the natural photoperiod regimens experienced by this species within its geographic range.

The upper range of the hatching period of the eggs collected during April to July (Fig. 47) greatly exceeded the maximum value (36 days) for egg hatch at 20°C, observed during the rate of development study (section 6.5.1.). The proportion of eggs, collected from the field on a specific date, that showed this 'delayed hatch' was similar at either the LD or SD photoperiods. This indicated that the 'delayed hatch' was not related to day length in the laboratory. The percentage of eggs that showed 'delayed hatch' was not constant, but changed with the date of collection (2.3% from 4 April; 13.4% from 27 April; 23.7% from 1 June; 0.4% from 2 July; and 0.3% from 30 July) which indicated that the response was not a simple inherited trait under genetic control.

The cause(s) of the increase in the percentage of eggs showing 'delayed hatch' up to the June collection was not evident in these experiments. The temperature regimen experienced in the field or perhaps stress (dessication or disease) may have played a role in affecting the response. However, the cause of the decrease of the percentage of eggs showing 'delayed hatch' after June was determined. The percentage of dead eggs (probably related to cold, dessication or disease which affected mainly the early embryos) increased markedly from 1 June to 2 July, from 9.7% (n = 237) to 47.3% (n = 203), respectively. Over the same period the percentage of eggs that hatched successfully in the laboratory decreased from 77.6% to 38.9%. Therefore, the reduction in the proportion of eggs showing 'delayed hatch' and in the range of the hatching period was probably caused by selective mortality of the eggs. It was not an indication of the completion of a dormancy period in the egg.

The lower range of the hatching period (Fig. 47) indicated that eggs, collected from the field, completed development some time between late April and early June. After 1 June some hatching usually occurred within 24 hours of setting up the eggs in the laboratory. Unlike the above, the results from the larval study indicated that eggs had hatched in the field by March in 1977 (cohort 3, Fig. 20). Stems collected 30 July, preserved immediately, and dissected in the laboratory showed that 9.7% of the eggs (n = 299) had already hatched. No stems were preserved before this; therefore, a similar check for an earlier collection date was not possible.

During 1978, in experiments similar to the above, eggs completed development by 12 February. Hatching in the laboratory was not observed until five days after the start of the experiment; however, stems preserved in the field and dissected in the laboratory showed that 4.2% of the eggs (n = 312) had already hatched by 12 February.

These results definitely showed that hatching had begun by mid-February in 1978. The same pattern probably occurred in 1977, but, perhaps because of a smaller sample size ($n \leq 10$ stems) the first hatch in the field may have gone undetected. The combined technique of egg incubation in the laboratory and dissection of stems preserved in the field may prove useful for further studies examining the development and hatching of eggs under natural conditions.

The incubation period for egg hatch 50% remained at about 15 to 17 days until 1 June, then decreased to two or three days after that (Fig. 47). The decrease coincided with the reduction in the upper limit of the hatching period caused by high mortality of the early embryos, as previously described. The value for egg hatch 50% decreased, not because of rapid development of the eggs in the field, but was caused because of selective mortality of the eggs.

The eggs collected on 10 September (Fig. 47) required at least 48 hours before hatching was noted in the laboratory and the incubation period for egg hatch 50% increased to six days from three days on 28 August. This, combined with the sudden decrease in the number of eggs hatching in the laboratory, was believed to indicate that a peak spring hatch of eggs had taken place before this collection, between 28 August and 10 September. Dissections of stems preserved in the field showed that the percentage of eggs hatched increased from 17.5% (n = 258) on 28 August, to 23.1% (n = 238) on 10 September. The hatch of a substantial portion of the older eggs in the population increased the value for egg hatch 50%, as observed. The air and water temperature records indicated no unusually high temperatures during this period (28 August to 10 September), nor was there an indication of heavy rainfall. The factors that induced hatching at this time are unknown.

The last hatching in the field occurred between 24 September and 9 October 1977. By 9 October only 25.2% of the eggs (n = 333) had hatched; the remainder died (57.1%) or remained undeveloped (17.7%).

6.5.3. Summary

The above factors and section 6.5.1. demonstrate that some eggs of *A. colensonis* do hatch the summer that they are laid, and that a spring hatch of eggs does occur at Lake Sarah - tb. Apparently the eggs do not respond to photoperiod nor do they rely upon a special dormant stage to ensure winter survival. The individuals that form the peak spring hatch are well developed embryos that survive the winter in a state of quiescence. A small portion of the population does respond to some unknown environmental factor(s), not photoperiod, and shows a 'delayed hatch' response. At Lake Sarah - tb; however, these individuals die during the winter. The hatching success of eggs collected early in the autumn 1977 varied from about 70 to 80%, but by late winter only about 25% of the eggs actually completed development.

6.6. *PROCORDULIA SMITHII*

6.6.1. Rate of Development

6.6.1.1. Results Observations made on eggs collected from five females at Lake Sarah - tb 13 February 1977 are presented in Table 19. These eggs were incubated at one temperature only, approximately 19.0°C, but at both photoperiods (LD and SD). The number of eggs laid by each female ranged from 222 to 1591.

Eggs used in experiments over a range of temperatures were obtained from one female collected at Lake Sarah - tb, 26 February 1978. It laid a total of 1413 eggs. The experimental conditions, developmental fate of the eggs and hatching periods are presented in Table 20.

All eggs developed directly at or above 20.0°C (group 1, see Fig. 48); however, at 19.1°C a small percentage of the population developed at a lower rate which produced a second mode of hatching (group 2), later in the hatching period. The percentage of the population that showed 'delayed hatch' increased at lower temperatures until at 15.6°C (Table 20) all the eggs fell into this category (group 2).

The linear regression lines were calculated for the relationship between rate of development and temperature for both groups in Table 20. From the equations for the lines (Fig. 48) the number of degree days for development to be completed was 161.3 and the threshold

TABLE 19. Egg study results for *Procordulia smithii*, 1977. Eggs incubated at approximately 19°C and LD or *SD photoperiods. Combined LD and SD pairs equals eggs from one female.

	Temperature (°C) (mean and range)		Number of Eggs	Hatching Success (%)	Dead Embryos (%)	Undeveloped Eggs (%)	Number of Eggs Hatched	Hatching Period (days after oviposition)	Egg Hatch 50% (days)
1	19.1±3	G 1	783	98.7	1.3	0	773	61-83	64
	-	G 2					-	-	-
	19.1±3*	G 1	808	98.5	1.5	0	774	65-113	69
	18.8±3*	G 2					22	135-271	240
2	19.1±3	G 1	160	88.1	11.9	0	141	62-125	67
	-	G 2					-	-	-
	19.1±3*	G 1	62	96.7	3.2	0	54	64-83	68
	18.8±3*	G 2					6	132-278	255
3	19.1±3	G 1	595	98.0	2.0	0	582	61-110	72
	18.9±3	G 2					1	235	235
	19.1±3*	G 1	536	93.7	6.3	0	500	64-84	66
	18.8±3*	G 2					2	143-225	143
4	19.1±3	G 1	288	100	0	0	288	61-105	63
	-	G 2					-	-	-
	19.1±3*	G 1	375	91.5	8.5	0	343	65-86	66
	-	G 2					-	-	-
5	19.1±3	G 1	365	99.7	0.3	0	364	62-101	65
	-	G 2					-	-	-
	19.1±3*	G 1	592	99.0	1.0	0	582	65-110	68
	18.7±3*	G 2					4	140-238	219

G 1 - group 1, eggs developed directly

G 2 - group 2, 'delayed hatch'

TABLE 20. Egg study results for *Procordulia smithii*, 1978. Eggs incubated at LD photoperiod except for *SD photoperiod, and + natural temperature and photoperiod at Lake Sarah - tb.

Temperature (°C) (mean and range)		Number of Eggs	Hatching Success (%)	Dead Embryos (%)	Undeveloped Eggs (%)	Number of Eggs Hatched	Hatching Period (days after oviposition)	Egg Hatch 50% (days)
24.6±1 1/2	G 1	22	95.5	0	4.5	21	16-22	17
-	G 2					-	-	-
20.0±1/2	G 1	1224	99.2	0.7	0.1	1214	20-35	22
-	G 2					-	-	-
19.1±2*	G 1	26	96.2	3.8	0	18	27-32	29
18.9±2*	G 2					7	187-207	188
18.0±1 1/2	G 1	19	89.5	10.5	0	1	101	101
17.9±2	G 2					16	159-195	186
-	G 1	22	77.3	22.7	0	-	-	-
15.6±1 1/2	G 2					17	221-267	246
-	G 1	13	15.4	84.6	0	-	-	-
10.8±4	G 2					2	260-295	260
-	G 1	14	78.6	14.3	7.1	-	-	-
8.3±2	G 2					11	260-309	288
-	G 1	9	44.4	33.3	22.2	-	-	-
7.5±1	G 2					4	261-359	261
12.9±5+	G 1	36	0	0	100	-	-	-
	G 2					-	-	-
Preserved Eggs		28	NOT INCLUDED IN THE EXPERIMENTS					

G 1 - group 1, eggs developed directly

G 2 - group 2, 'delayed hatch'

Fig. 48. Relationship between temperature and rate of development for egg hatch 50% of *Procordulia smithii*. The equations and calculated linear regression lines are shown.

Symbols:

circles - fast developing group 1.

triangles - 'delayed hatch' group 2.

hollow - SD photoperiod.

solid - LD photoperiod.

Fig. 49. Response of 'delayed hatch' eggs of *P. smithii* to day length change and prior exposure to cold (6°C).

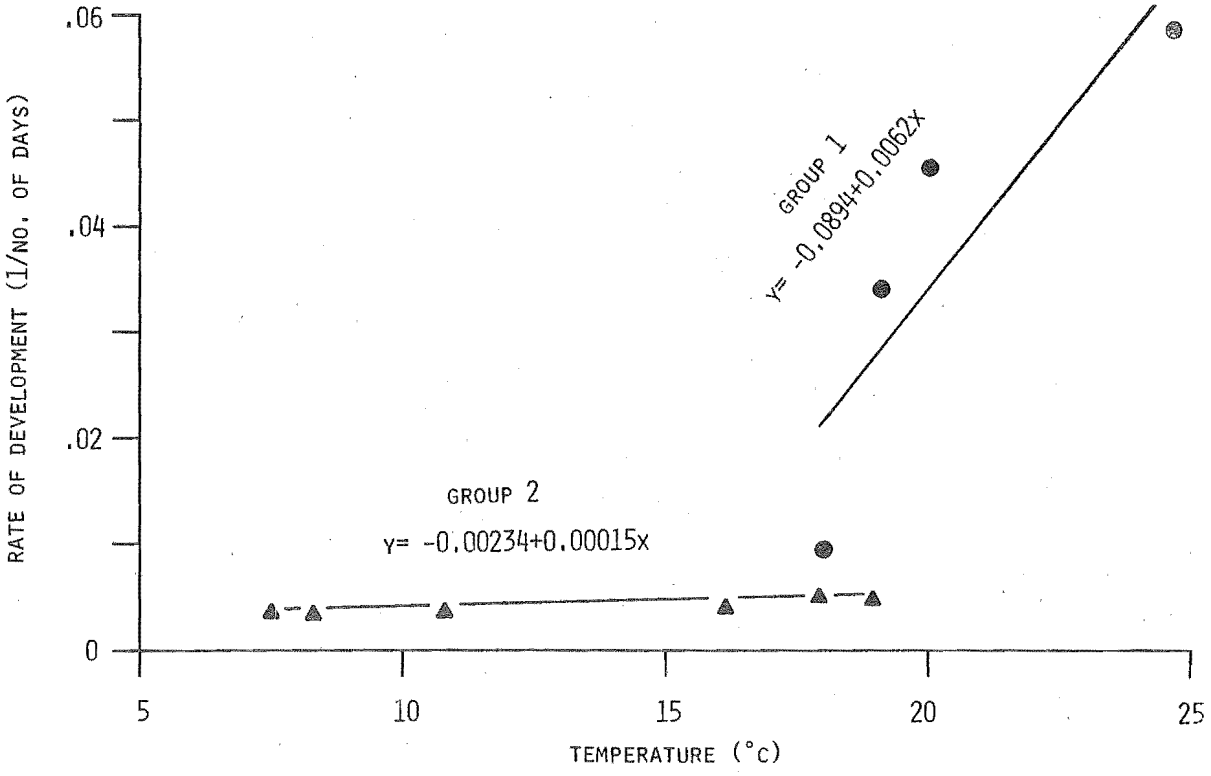
Sybmols:

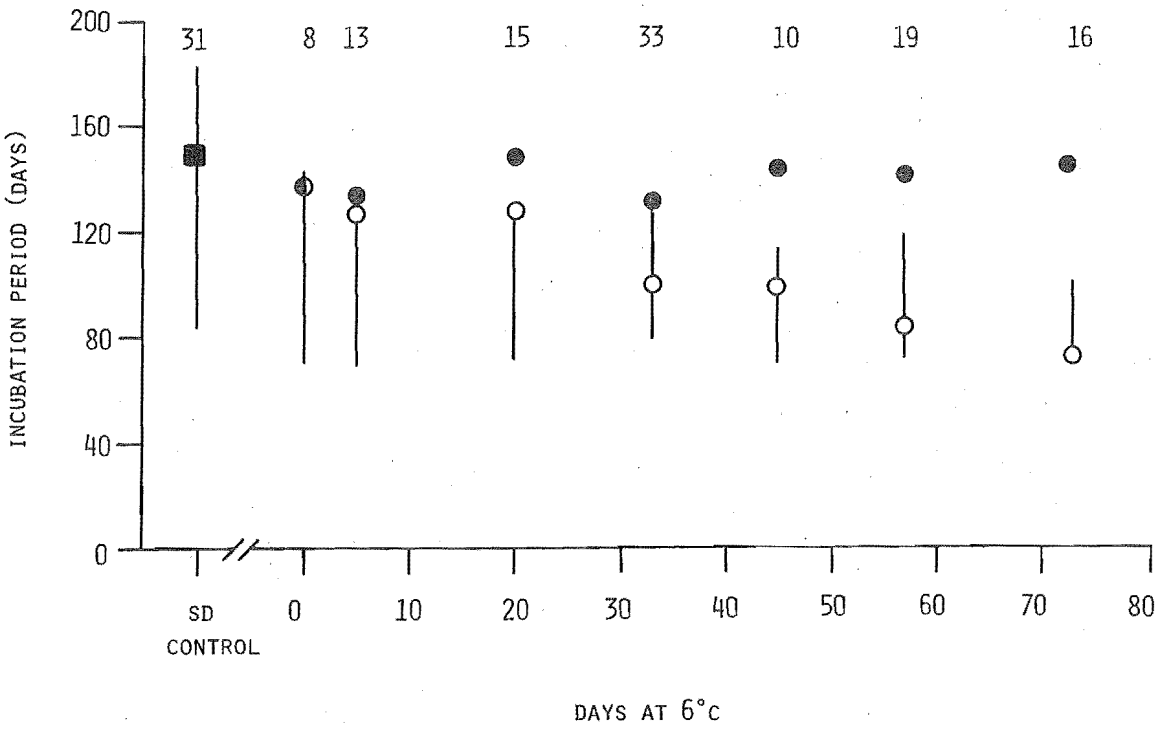
hollow circles - incubation period at 20°C.

solid circles - overall incubation period.

squares - SD 20°C control.

The range of the hatching period for the eggs incubated at 20°C is indicated. Upper numbers show the number of eggs hatched.


RATE OF DEVELOPMENT (1/NO. OF DAYS)
.06
.04
.02
0
GROUP 1
Y= -0.0894+0.0062X
GROUP 2
Y= -0.00234+0.00015X
5
10
15
20
25
TEMPERATURE (°C)


INCUBATION PERIOD (DAYS)
200
160
120
80
40
0
31
8
13
15
33
10
19
16
SD
CONTROL
0
10
20
30
40
50
60
70
80
DAYS AT 6°C

temperature was 14.4°C for group 1, whereas for group 2 the number of degree days for development to be completed was 6666.7 and the threshold temperature was -15.6°C.

6.6.1.2. Comments The number of eggs laid per female, up to 1591, is much higher than that observed for the two zygopteran species studied. The large batch size of *P. smithii* is a feature that is common to the Odonata that deposit eggs exophytically. Individuals of various exophytic species have been reported to lay anywhere from 150 to over 5000 eggs in one batch (see Table II, p.29, Corbet 1962).

As mentioned, the eggs of *P. smithii* developed at two different rates depending on the temperature regimen experienced (Fig. 48). Between 20.0 and 15.6°C the response of eggs changed from one of rapid development to one of 'delayed hatch'. However, my initial impression from previous work (Table 19) was that the eggs of *P. smithii* went into an obligatory diapause, because the eggs required 64 to 72 days to complete egg hatch 50% at 19.1°C in both the LD and SD photoperiods. The small 'delayed hatch' group went unrecognised in 1977. Therefore, the experiments in 1978 were designed to examine the nature of this suspected obligatory diapause. Most of the eggs were set up at LD 20°C to provide material for later studies. These eggs all developed directly and completed hatching within 35 days (Table 20). The number of days required by eggs to complete egg hatch 50% at SD 19.1°C in 1977 (Table 19) differed markedly from that of eggs in 1978 (Table 20), probably because of larger temperature fluctuations experienced during the 1977 experiments.

It appeared that an exposure to temperatures below 20°C, even for a brief period, resulted in a marked rate change in development. The change in the response of eggs to temperature was extreme in the range from 20 to 18°C (Fig. 48). With the larger temperature fluctuations in 1977 the eggs were exposed to lower temperatures than experienced in 1978. The eggs in 1977 probably developed more slowly as a result of the extreme response to temperatures below 20°C.

The interpretation of the results from 1978 can now be attempted, but they must be considered tentative because of the nature of the experiments. More temperature conditions between 15 and 25°C, better control of temperatures, more eggs in the experiments, and eggs from different individuals, perhaps collected at different times during the season are required before definite conclusions can be made about the

nature of the egg response of this species.

The linear regression line calculated for group 1 (Fig. 48) indicated that the threshold temperature was 14.4°C. The results (Table 20), however, indicated that the true threshold temperature occurred between 15.6 and 18.0°C. A log-log, or some other form of transformation of these results may provide a better description of the relationship between rate of development and temperature and give a more realistic estimate of the threshold temperature. However, because of the small number of results around the critical temperature, such analyses are not possible with any degree of reliability at this time. More information is necessary before further comment can be made.

The results for group 1, the fast developing group of eggs, indicated that there was no difference in response to the LD and SD photoperiod conditions (Fig. 48). This was also observed in 1977 (Table 19). The eggs developed at the same rate in both photoperiods at 19.1°C.

The results for the 'delayed hatch' group of eggs (Fig. 48 & Table 20) indicated hatching to be almost independent of temperature. The relationship is probably linear as designated (Fig. 48); however, what happens between 7.5°C, lowest experimental temperature, and -15.6 C the calculated threshold temperature, is unknown. Again, more information is needed before definite comments can be made about the nature of this response.

The hatching success of *P. smithii*, approximately 75% to 100%, (Tables 19 & 20) was similar to that of *X. zealandica* (section 6.4.1.2.). The same relationship between low temperature and an increase in the number of dead and undeveloped embryos was observed, as previously noted for *X. zealandica* (section 6.4.1.2.) and *A. colensonis* (section 6.5.1.2.), but because of the small sample size of *P. smithii* eggs at the lower temperatures (Table 20) this must again be considered as a tentative observation only.

Eggs that were set up in the field at Lake Sarah - tb failed to develop (Table 20). They were probably affected in the manner previously described for *X. zealandica* (section 6.4.1.2.) which resulted in the death of the eggs.

6.6.2. 'Delayed Hatch'

After the 'delayed hatch' group of eggs was recognised in 1978, attempts were made to clarify the nature of this unusual response.

Firstly, the stage of embryonic development affected was determined by visual examination of eggs that were known to belong to the 'delayed hatch' group. Eggs from several experiments were examined at 50 X total magnification, using a Wild M5 dissecting microscope and dark field illumination.

Secondly, the effect of photoperiod changes and of exposure to cold was examined. 'Delayed hatch' eggs (n = 32), obtained from one female collected at Lake Rotoaira, 13 February 1978, and one female collected near Hunterville, 15 February 1978, were transferred from SD 20°C, after 68 days, to LD 20°C to simulate the day length change from winter to summer. Eggs from these females were also used to determine the effect of exposure to cold on 'delayed hatch'. Two hundred and twenty-eight eggs incubated at LD and SD 20°C for 68 days were transferred to LD 6°C. The 6°C temperature was selected to represent the cool conditions experienced by *P. smithii* eggs in the field during 'delayed hatch'. After 5, 20, 33, 45, 57, and 73 days exposure to these cool conditions at least 30 eggs were moved to LD 20°C to complete development.

6.6.2.1. Results By the time that 'delayed hatch' eggs could be recognised the embryos were already full grown. The compound eyes were black, the tracheal system was noticeably differentiated and the claws were separated from the tarsi by a clearly formed junction; see stages 12 and 13 of Ando (1962, p.66).

The results of the Lake Rotoaira and Hunterville egg transfers were similar for each female; therefore, the data were pooled for presentation in Fig. 49. The overall incubation period from the time that the experiments were set up to egg hatch 50% remained at about 130 to 150 days for all the groups (Fig. 49). The incubation period at 20°C from the time that the experiments were set up to egg hatch 50% decreased at a rate approximately equivalent to the period of exposure to 6°C. As exposure to 6°C increased the subsequent range of the hatching period decreased and egg hatch 50% occurred earlier during the hatching period at 20°C.

6.6.2.2. Comments Although the embryos were apparently fully developed, 'delayed hatch' eggs often failed to hatch for many months. The hatching delay was not merely a prolongation of embryonic development, but was probably a true egg diapause, possibly of the type

described by Ando (1962, p.73) for *Sympetrum* eggs.

The similarity of the overall incubation period for all the groups, including the SD 20°C control group (Fig. 49), indicated that the change in day length or exposure to 6°C had little, if any, effect on promoting egg development. As mentioned earlier (section 6.6.1.) more eggs undergo 'delayed hatch' = diapause with decreasing temperature from approximately 19°C. Once initiated diapause continued regardless of photoperiod changes (Fig. 49) and surprisingly development continued at about the same rate at either 6 or 20°C. Perhaps this constant rate of development supports the observation that hatching of the 'delayed hatch' group is almost independent of temperature (section 6.6.1.2.); or alternatively these rates at 6 and 20°C could occur on either side of the optimum temperature for the completion of diapause development. A detailed study is needed to clarify the nature of diapause in *P. smithii* eggs.

The increasingly early occurrence of egg hatch 50% at 20°C and the decrease in the range of the upper limit of the hatching period (Fig. 49) indicated that development of the embryos continued to take place at 6°C. Also, the constancy of the lower limit of the hatching period, never earlier than two days after re-exposure to 20°C, was believed to indicate a threshold temperature for hatching. After 73 days exposure to 6°C hatching occurred synchronously when the eggs were returned to 20°C. Because some hatching occurred in the laboratory at 7.5°C (Table 20) the threshold temperature for hatching of *P. smithii* eggs must fall between 6 and 7.5°C contrary to the -15.6°C calculated in section 6.6.1.

6.6.3. Summary

The results from the previous sections indicate the presence of an egg diapause in *P. smithii* that apparently is induced by temperature. If eggs are laid in areas where the temperature seldom falls below about 19°C then hatching can occur the summer that they are laid. Otherwise eggs overwinter and hatch synchronously the following spring when the water temperature reaches the critical level between 6 and 7.5°C. At Lake Sarah - tb most eggs would respond in the latter fashion (overwinter), as supported by earlier results (section 4.5.1.).

6.7. *PROCORDULIA GRAYI*

6.7.1. Rate of Development

6.7.1.1. Results The eggs used in these experiments (Table 21) were obtained from one female collected at Lake Sarah, 21 January 1978. It laid a total of 614 eggs. The experimental conditions, developmental fate of the eggs and hatching periods are presented in Table 21. The linear regression line for the relationship between rate of development and temperature was calculated using the results, excluding the SD photoperiod group. From the equation for this line (Fig. 50) the number of degree days for development to be completed was 192.3 and the threshold temperature was 9.5°C.

TABLE 21. Egg study results for *Procordulia grayi*. Eggs incubated at LD photoperiod except for * SD photoperiod, and + natural temperature and photoperiod at Lake Sarah - tb.

Temperature (°C) (mean and range)	Number of Eggs	Hatching Success (%)	Dead Embryos (%)	Undeveloped Eggs (%)	Hatching Period (days after oviposition)	Egg Hatch 50% (days)
20.0±1/2	104	99.0	0	1.0	17-24	18
19.8±2*	94	98.9	0	1.1	20-32	26
18.6±2 1/2	69	97.2	1.4	1.4	19-22	20
15.9±1	61	98.4	0	1.6	38-39	39
11.9±4	53	94.3	0	5.7	63-72	64
8.7±3	76	0	34.2	65.8	-	-
7.7±2	61	0	24.6	75.4	-	-
15.5±5+	96	0	0	100	-	-

* 10L:14D photoperiod, all the rest at 16L:8D regimen.

6.7.1.2. Comments The number of eggs laid by the *P. grayi* female (614) falls within the range observed for *P. smithii* (section 6.6.1.1.).

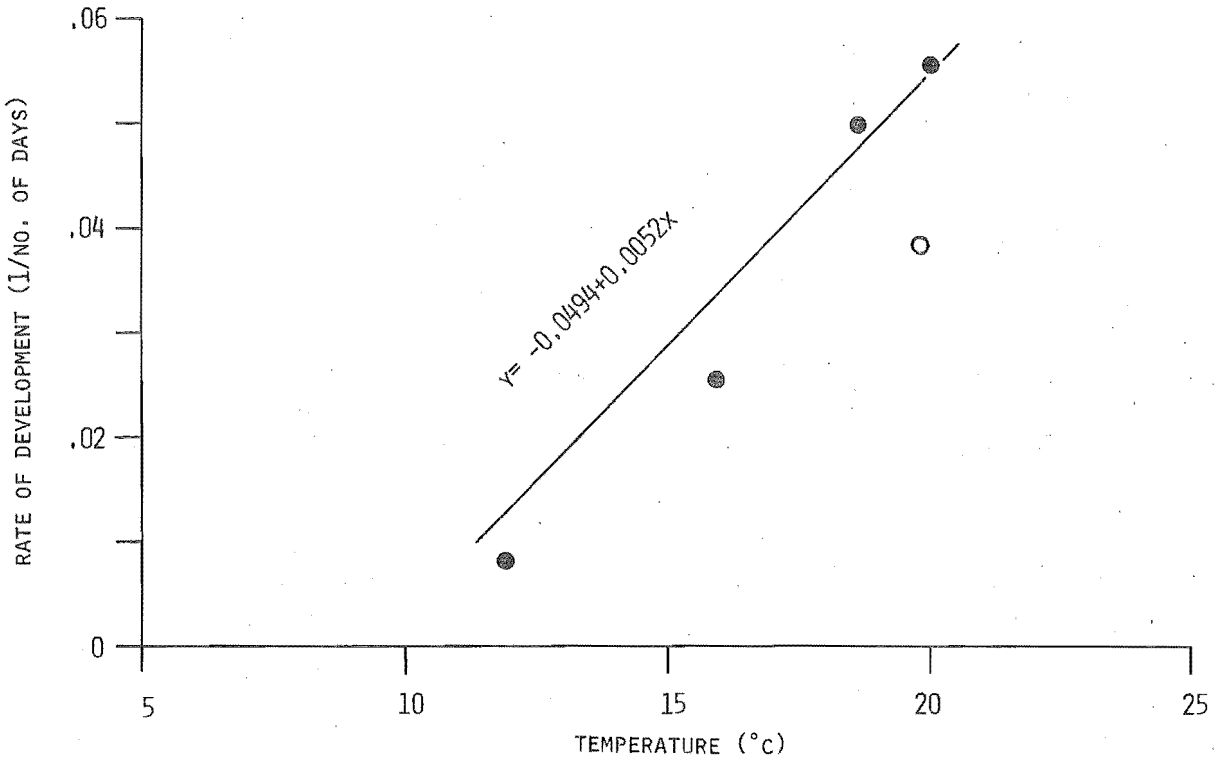
The eggs of *P. grayi* developed directly within the temperature range from 20.0 to 11.9°C, but at temperatures below the threshold temperature (9.5°C) no eggs hatched and an increasing number of eggs remained undeveloped (Table 21). This relationship between undeveloped eggs and low temperature was also observed in *X. zealandica* and

Fig. 50. Relationship between temperature and rate of development for egg hatch 50% of *Procordulia grayi*. The equation and calculated linear regression line are shown.

Symbols:

hollow circles - SD photoperiod.

solid circles - LD photoperiod.


.06
.04
.02
0
5
10
15
20
25
RATE OF DEVELOPMENT (1/NO. OF DAYS)
TEMPERATURE (°c)
Y= -0,0494+0,0052x

A. colensonis, and may have occurred in *P. smithii*. Perhaps it is a characteristic feature of embryonic development within the Order.

The linear relationship between the rate of development of the eggs and water temperature was significant ($P<0.05$) when determined with or without the SD photoperiod group. The regression line calculated without the SD photoperiod group showed a better agreement with the data. This line is presented here. The results from the SD photoperiod group fell outside the 95% confidence limits calculated for 19.8°C. This was believed to indicate that the eggs of *P. grayi* do respond to photoperiod. The response, however, appears to be simply a prolongation of development rather than a dormant state. The eggs took about seven days longer to complete development than expected. In the LD photoperiod groups temperature appeared to be the major factor regulating the rate of development. All the eggs died at 8.7 and 7.7°C (Table 21) indicating that the calculated threshold temperature represents a real biological limit for the development of the eggs of *P. grayi*.

Eggs that were set up in the field at Lake Sarah - tb failed to develop (Table 21). They were probably affected in the manner previously described for *X. zealandica* (section 6.4.1.2.) which resulted in the death of the eggs.

6.7.2. Summary

The above observations must be considered as tentative only. They were based on evidence obtained from one individual and no field observations were available to support them. With this in mind the results indicate that the eggs hatch the summer that they are laid and may show a slight response to photoperiod (SD prolongs development). A true dormant stage (diapause) was not detected.

7. LARVAL GROWTH STUDY

7.1. INTRODUCTION

The larval study was carried out for the following reasons.

Firstly, it was designed to investigate possible growth restrictions in the larvae noted in the larval surveys. Examples of these are taken from the larval survey summary sections, *i.e.* the possible growth restrictions in:

- the later instar larvae of *X. zealandica* at Isaac's Pond and Lake Sarah - tb (sections 4.3.1.3 & 4.3.2.3.);

- the F-2 instar larvae of *A. colensonis* at Lake Sarah - tb (section 4.4.1.3.); and

- the F-1 instar larvae of *P. smithii* at Lake Sarah - tb (section 4.5.1.3.).

By means of experimentation in the laboratory the inferences about the growth restrictions were either confirmed or refuted. As mentioned previously (section 1.) most effort was directed towards the study of *X. zealandica*. The normal (non-diapause) growth and development of selected instars of *X. zealandica* was followed in the laboratory at various temperatures. From these results, the temperature at which the developmental rate was zero, (*i.e.* the threshold temperature) was determined and the maximum duration for normal development was calculated for each instar. A second experiment examined the relationship between day length (SD and LD) and prey consumption as a possible factor affecting growth. Finally the pattern of response to the LD and SD photoperiods was determined for larvae collected from the field at monthly intervals during a one-year period and the growth restrictions, if any, and the larval instars affected were identified.

The second reason for the larval study was to examine the nature of the confirmed growth restrictions. This information was provided by the above experiments. The identification of the principal factors regulating the growth restrictions was attempted when possible.

7.2. METHODS AND ANALYSES

7.2.1. Larval Collection and Handling

Larvae were collected in the manner described for the regular

monthly samples (section 4.2.1.), sorted fresh (section 4.2.3.), and stored at room temperature. Each larva was placed separately in a clear glass vial (internal diameter 17mm; height 42mm) to prevent cannibalism. After all the samples were sorted, the larvae were positively identified, measured and assigned to instars (section 2.), then transferred to approximately 150ml of aged, oxygenated tap water at room temperature in clear glass jars (height 90mm, internal diameter 60mm). Prey, the lumbriculid worm *Lumbriculus variegatus* (Müller), was provided *ad libitum*. The jars were placed in white plastic trays for storage and stacked in the cabinets at the appropriate experimental conditions (section 6.2.). Any deviations from the above procedure are mentioned in the appropriate section.

7.2.2. Maintenance and Termination

Larvae were checked for moults, early metamorphosis (see section 4.2.5.), emergence, or deaths at three-day intervals and food (*L. variegatus*) and water were added as required. Exuviae, emerged adults, or dead larvae were placed in numbered vials and preserved in 70% alcohol plus 1% glycerine for future reference. The duration (in days) was noted from the start of the experiment in the laboratory to the time of the first moult, early metamorphosis and emergence, or death of each individual. Larvae that were suspected of supplementary (supernumerary) moulting (see pp. 6 & 180) were maintained to obtain a definite instar identification. The non-metamorphosis portion of the F instar provided information about development without complications arising from mortality associated with metamorphosis and emergence.

Larvae in metamorphosis were provided with a piece of *Typha* stem which served as an emergence site.

Larvae were counted as dead if unresponsive to a touch stimulus, or if decay was obvious. If the condition of the animal was uncertain then it was left for re-examination at a later date.

7.2.3. Experimentation

7.2.3.1. Normal rate of development This experiment was carried out at a time of the year (spring) when the larvae were believed to be developing at a 'normal' (non-diapause) rate as indicated by the larval survey (section 4.). Larvae of *X. zealandica* in the F-3 to

F-1 instars, and larvae of *A. colensonis* in the F-4 to F-1 instars were collected from Lake Sarah - tb, 16 October 1977. These larvae were set up at LD, approximately 17°C and checked at 12- hour intervals for moulting. Newly moulted larvae were assigned to an instar and immediately set up at the LD photoperiod at approximately 25, 20, 17.5, 15, 12.5, 10 or 7.5°C. Larvae in the first four conditions were checked at 12- hour intervals and in the last three conditions were checked at 24- hour intervals until they moulted into the subsequent instar, reached early metamorphosis then emerged, or died.

Each of the instars (F-3 to F-1) was treated as a developmental unit, except for the F instar which was divided into two stages (non-metamorphosis and metamorphosis, see section 7.2.2.). No attempt was made to identify separate developmental stages within each instar, as was done by Norling (1976), because this was considered beyond the scope of this project.

7.2.3.2. Prey consumption F instar larvae of *X. zealandica*, *A. colensonis* and *P. smithii* were collected at Lake Sarah - tb, 30 July 1977, and set up at LD or SD 20°C. Unlike the other experimental groups these dragonflies were fed a known number of F instar larvae of the mosquito *Opifex fuscus* Hutton (15 mosquito larvae to one *P. smithii* larva and 10 mosquito larvae to one zygopteran larva per day). The number of prey consumed was determined at 24- hour intervals and mosquito larvae were added to return the prey density to the required level. The experiment was continued until the dragonflies emerged or died.

7.2.3.3. Seasonal response to photoperiod These experiments were carried out using the later instar larvae; (F-2 to F) of *X. zealandica*, (F-2) of *A. colensonis*, and (F-1) of *P. smithii*, as available. Experiments with larvae from Lake Sarah - tb were started 21 February 1977 and continued at approximately monthly intervals to 26 February 1978. Experiments with *X. zealandica* larvae from Isaac's Pond were started 2 August 1977 and continued to 27 April 1978. The above larvae were set up in LD and SD 20°C and maintained as described earlier (section 7.2.2.).

7.2.4. Analyses

7.2.4.1. Normal rate of development These experiments were analysed using techniques similar to those described earlier (*i.e.*,

linear regression analysis, section 6.3.3.). Each observation, the reciprocal of the time (in days) for the successful completion of a given stage of development, was used in the calculation of the equation for the line, from which was determined the number of degree days for development to be completed and the threshold temperature. The maximum duration for normal development of each instar tested and for metamorphosis of *X. zealandica* and of *A. colensonis* at 20°C was calculated at a probability level of 0.05. This was obtained from the transformed equation of the *t* - test for the comparison of a single specimen with a sample (see p.183, Simpson, Roe & Lewontin 1960).

$$X_{max} = \bar{X} + \frac{t\ s}{\sqrt{\frac{N}{N+1}}}$$

N - number of observations in the sample at 20°C.

s - standard deviation (days) of the sample at 20°C calculated from the 95% confidence limits of the linear regression line.

$$s = \frac{L_1(\text{days}) - L_2(\text{days})}{1.960} \qquad \sqrt{N}$$

t - Student's *t* value at a probability level of 0.05 for N-1 degrees of freedom.

$\bar{X}$ - mean duration (days) of the sample at 20°C calculated from the linear regression line.

X_{max} - the maximum duration (days) for normal development at 20°C. When calculated at a probability level of 0.05 only 5% of the observations could be expected to require developmental periods longer than or equal to this value to complete development.

X_{max} was rounded off to the nearest whole integer value, because observations in later studies were made as whole integers. Responses, observed in the seasonal response to photoperiod study, that were greater than or equal to X_{max} were considered indicative of prolonged (non-normal) development.

7.2.4.2. Prey consumption Observations were started two days after the start of the experiment and back calculated to end five days before emergence or death to obtain relatively standardised feeding rates. The number of *O. fuscus* larvae eaten per individual

per day was combined to form a series of observations for the LD photoperiod group and for the SD photoperiod group. Equal numbers of observations were included in each group. The two samples were tested for differences using the Mann-Whitney U test (two-tailed at a probability level of 0.05) (Siegel 1956).

7.2.4.3. Seasonal response to photoperiod The responses of the larvae in each of the LD and SD experiments were classified into either normal or prolonged (non-normal) development groups based on the X_{max} value (see section 7.2.4.1.). The percentage mortality, which included the larvae that died before the completion of development to the subsequent instar, and the percentage of the larvae showing normal development in each experiment were calculated and graphed. Because the larvae were of an unknown age when collected and set up in the laboratory, (see also p.147) the observed percentage of the larvae showing normal development must be considered a maximum value, perhaps over-estimating the true value. Larvae that died before moulting, but exceeded the X_{max} value, were included in the prolonged development group, as were larvae that exhibited supplementary moulting.

The standardised procedures of these experiments were considered to provide results that were directly comparable from month to month. These results indicated not only the developmental state of the larvae in the field at the time of collection but also the response of the larvae to the LD and SD photoperiods during the year. The mean duration (in days) of the larval response (± one standard deviation) was calculated and graphed for each of the normal and prolonged development groups in the LD and SD conditions. Observations on larvae that died before moulting but exceeded the X_{max} value and on larvae that exhibited supplementary moulting were not included in these calculations.

7.3. *XANTHOCNEMIS ZEALANDICA*

7.3.1. Normal Rate of Development

7.3.1.1. Results The numbers of larvae obtained for distribution among the seven temperature conditions, their percentage mortality, the degree days, threshold temperature and maximum duration for normal development at 20°C (X_{max}) of larvae in the instars F-2, F-1, and F up to early metamorphosis, and from early metamorphosis to

emergence, are presented in Table 22. The linear regression line for the relationship between rate of development and temperature and the equation for this line is presented for the above instars in Figs. 51 to 54.

TABLE 22. Normal rate of development in the LD photoperiod of *Xanthocnemis zealandica* larvae.

Instar or Stage	Number set up	Mortality (%)	Degree Days Required to Complete Instar or Stage	Threshold Temperature (°C)	X_{max} (days) at 20°C (P = 0.05)
F-2	39	72	243.9	9.6	63
F-1	62	48	454.5	3.8	44
F to early meta-morphosis	62	32	192.3	7.6	23
F from early meta-morphosis to emerg-ence	42	19	100.0	8.9	13

7.3.1.2. Comments The mortality of the stages tested (Table 22) was highest in the F-2 instar and decreased to lowest in the F instar larvae during metamorphosis. Apparently the early instar larvae were not as 'hardy' as the later instar larvae. The results obtained in experiments with the F-2 instar larvae must be treated as provisional because of this high mortality.

The linear relationships between the rate of development of the various stages tested and temperature (Figs. 51 to 54) were all highly significant ($P<0.001$).

The threshold temperature for development of F-2 instar larvae was calculated to be 9.6°C; however, one larva was observed to complete development at 8.6°C (Fig. 51). This is an indication that the calculated threshold temperature is too high, probably because of the small sample (especially at the lower temperatures) from which the linear regression line was calculated (Fig. 51). Similarly, the small sample at 20°C (n = 3) resulted in an artificially high X_{max} value (63 days). The reliability of this value as an indication of prolonged development is discussed in section 7.3.3.2..

Fig. 51. Relationship between temperature and rate of development of *Xanthocnemis zealandica* F-2 instar larvae. The equation and calculated linear regression line with 95% confidence limits are shown.

Fig. 52. Relationship between temperature and rate of development of *Xanthocnemis zealandica* F-1 instar larvae. The equation and calculated linear regression line with 95% confidence limits are shown.

Fig. 53. Relationship between temperature and rate of development of *Xanthocnemis zealandica* F instar larvae up to early metamorphosis. The equation and calculated linear regression line with 95% confidence limits are shown.

Symbols:

solid circles - one observation

hollow circles - two observations

hollow circles with central dot - three observations.

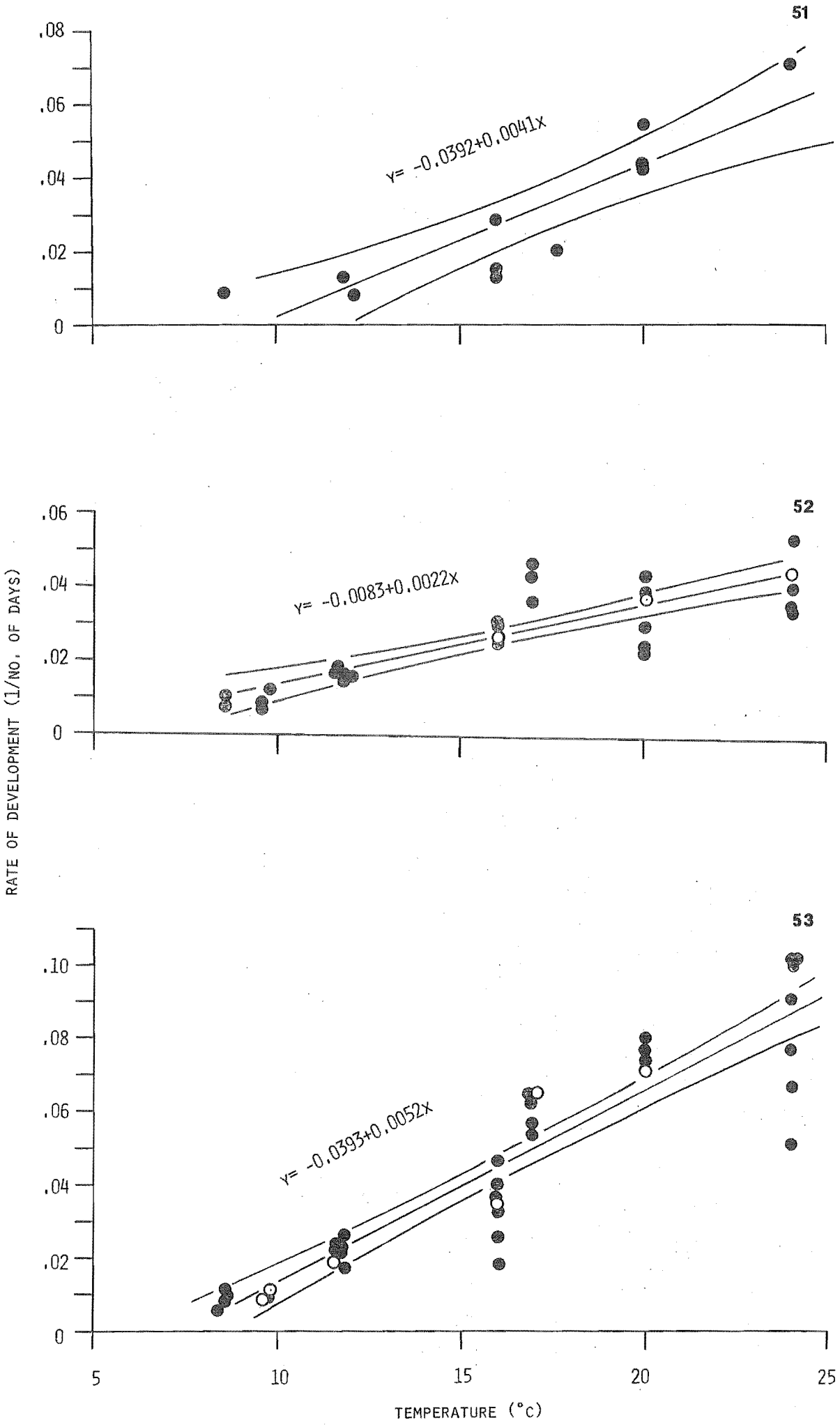

51
.08
.06
.04
.02
0
Y= -0.0392+0.0041x
52
.06
.04
.02
0
Y= -0.0083+0.0022x
53
.10
.08
.06
.04
.02
0
Y= -0.0393+0.0052x
5
10
15
20
25
TEMPERATURE (°C)
RATE OF DEVELOPMENT (1/NO. OF DAYS)

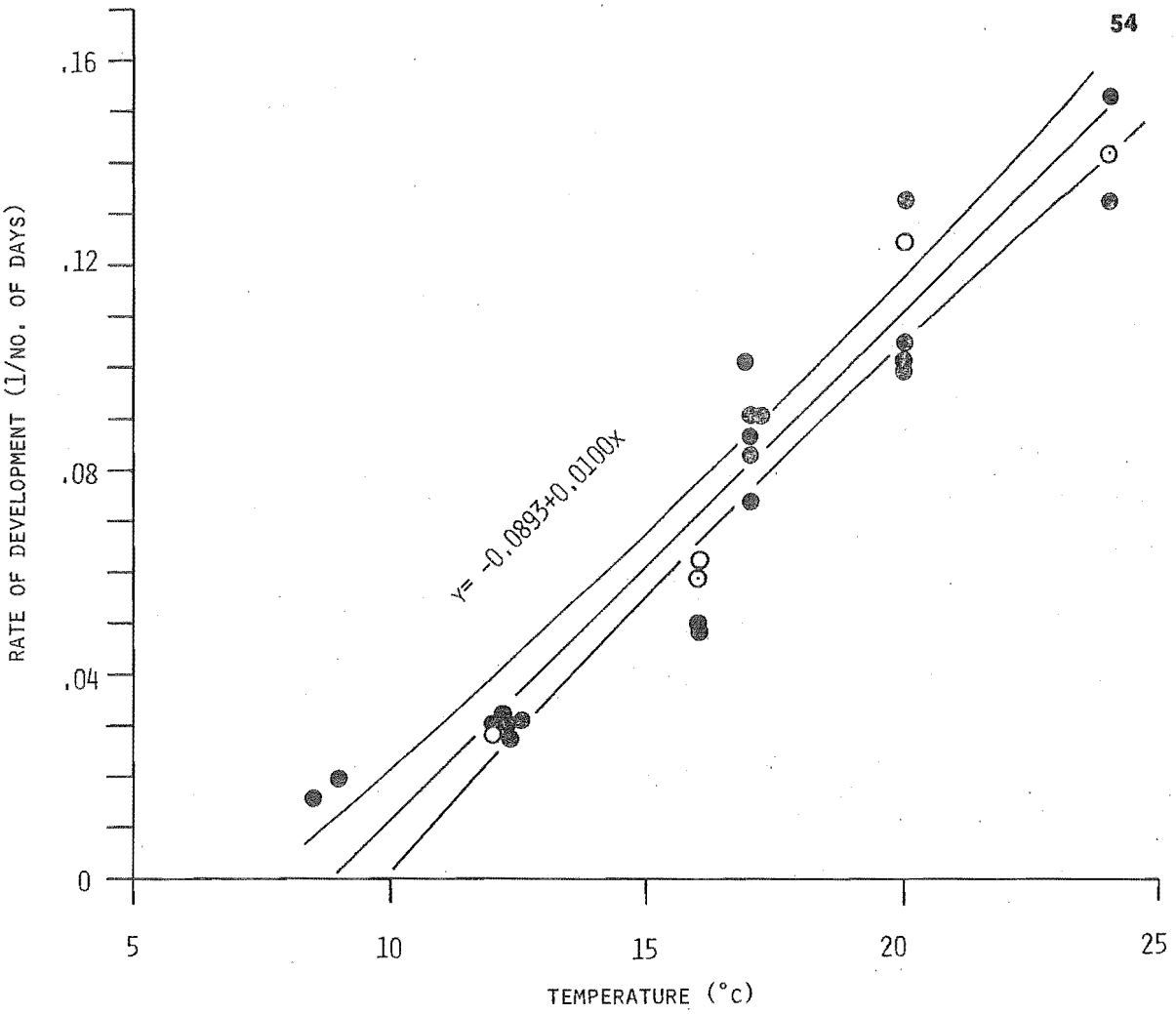
Fig. 54. Relationship between temperature and rate of development of metamorphosis in *Xanthocnemis zealandica*. The equation and calculated linear regression line with 95% confidence limits are shown.

Symbols:

solid circles - one observation

hollow circles - two observations

hollow circles with central dot - three observations.


.16
.12
.08
.04
0
5
10
15
20
25
RATE OF DEVELOPMENT (1/NO. OF DAYS)
TEMPERATURE (°C)
Y= -0.0893+0.0100x

The threshold temperature for development of F-1 instar larvae was calculated to be 3.8°C; however, mortality experienced in this instar increased with decreasing temperature. At 8.6°C five of seven larvae died (71% mortality) before completing development. This may indicate that the calculated threshold temperature is too low. The true threshold probably lies somewhere between 3.8 and 8.6°C. The X_{max} value at 20°C (44 days) is based on a sample of eight and is probably a reasonable estimate of the true value as discussed in section 7.3.3.2..

The threshold temperature for development of F instar larvae up to early metamorphosis was calculated to be 7.6°C. Neither growth of larvae in the laboratory nor mortality trends indicated any error in this estimate. Similarly, the X_{max} value at 20°C (23 days) (n = 5) is also believed to be a reasonable estimate of the maximum duration for normal development as discussed in section 7.3.3.2..

The threshold temperature for development of F instar larvae from early metamorphosis to emergence was calculated to be 8.9°C; however, one larva emerged at 8.4°C (Fig. 54), indicating that the calculated threshold temperature is too high. Mortality during metamorphosis occurred only at temperatures below 12°C in these experiments. Larvae at cool conditions reached an advanced state of metamorphosis and then died without completing emergence. Only two larvae out of thirteen emerged successfully at 9.0 and 8.4°C. The threshold temperature probably lies close to 8.4°C because of the high mortality at this temperature. The X_{max} value at 20°C (13 days) (n = 6) is believed to be a reasonable estimate as discussed in section 7.3.3.2..

The threshold temperatures for development of all the stages tested probably falls between 7 and 9°C. This supports the results obtained for larval growth in the field during the winter at Isaac's Pond and Lake Sarah - tb presented in sections 4.3.1. and 4.3.2., respectively. Growth would continue at Isaac's Pond during the winter. At Lake Sarah - tb, which experienced water temperatures of around 4°C, growth would not occur until the following spring.

Although the threshold temperature probably applies only to a specific temperature - sensitive stage within a given instar, this does not affect the above conclusions. Development within the entire instar was examined; therefore, the sensitive stage was detected. Growth would continue in a particular instar up to this stage only. The

response of larvae to temperature would probably be similar in the field or in the laboratory.

7.3.2. Prey Consumption

7.3.2.1. Results Observations were made on five larvae (number of observations = 69) in the LD, and five larvae (number of observations = 69) in the SD photoperiod conditions. The mean and one standard deviation of the number of *O. fuscus* larvae eaten per individual per day was 1.22 ± 0.74 in the LD photoperiod conditions and 1.26 ±0.90 in the SD photoperiod conditions.

7.3.2.2. Comments The critical U-value was 2443.5 and the calculated U-value was 2840.8, which indicated that there was no significant difference ($P>0.05$) between the feeding rates of the larvae in the two samples. Prey consumption was apparently not related to the day lengths tested; therefore, this relationship could be eliminated as a possible factor affecting the developmental rate of the larvae.

7.3.3. Seasonal Response to Photoperiod

Space in the laboratory limited the maximum size possible of each instar group to about 10 individuals in each photoperiod per collection. At certain times additional space was available and more larvae were used; however, larvae of an appropriate instar occasionally were difficult to find at particular periods during the year and fewer larvae were used. The number of observations for a specific instar on a particular date often were small ($n<10$), especially after mortality reduced the initial number of larvae in the experiments. Therefore, the conclusions drawn from these experiments must be treated as being provisional because of small sample size.

The strength of the experimental design used here was that it provided the general response trends of the population during the year. Seasonal patterns of response were obtained more from a series of experiments than from solitary observations; therefore, to a certain degree, this approach negated the error arising from small sample size (see above).

Lutz & Jenner (1964) carried out studies of a similar nature with *T. cynosura* in long day (14L:10D) and short day (11L:13D) photoperiods at 22°C during a nine-month period (August to April) when

later instar larvae were present in the field. In this study and later, with additional species and/or temperatures (Lutz 1968b, 1974a, 1974b), the advantage of this approach is clearly evident, *i.e.* the seasonal changes in the response of larvae to photoperiod are easily recognised.

7.3.3.1. Results - Lake Sarah - tb F-2 instar Larvae were last collected in the 1977 cohort on 30 October 1977 and did not appear in the 1978 cohort until the collection of 8 January 1978. The percentage mortality and the percentage of the larvae showing normal development, based on X_{max}, is presented in Figs. 55 & 56 for the LD and SD photoperiods, respectively.

Mortality was noticeable during two periods:

- from 21 February to 2 July 1977; and
- from 8 January to 26 February 1978 (Figs. 55 & 56).

However, in the experiments from 30 July to 30 October 1977, all the larvae survived.

About 60 to 80% of the larvae collected on 21 February and 20 March 1977 (Figs. 55 & 56) developed normally, whereas almost all the larvae developed normally from 27 April until 30 October 1977. Few larvae in the 1978 cohort developed at the normal rate during January 1978, especially in the LD photoperiod (Fig. 55). By 26 February 1978 this proportion increased in the LD group (Fig. 55) but decreased in the SD group (Fig. 56).

The mean duration for development in the F-2 instar normal development group (Fig. 57) was similar at both photoperiods for a given date from 21 February to 30 October 1977, excluding the observations from 27 April 1977 because of small sample size (n = 2). The mean duration for development decreased during the period from 28 August to 30 October 1977.

The larvae in the 1978 cohort in the normal development group showed a differential response to the LD and SD photoperiods during January 1978 (Fig. 57).

The mean duration for development in the F-2 instar prolonged development group (Fig. 57) was similar at both photoperiods, about 70 to 80 days. Prolonged development was observed mainly during the period from January to March. One larva, collected 1 October 1977, showed prolonged development outside this period.

Fig. 55. Percentage mortality and percentage of the larvae showing normal development in the F-2 instar of *Xanthocnemis zealandica* from Lake Sarah - tb, maintained at LD 20°C.

Fig. 56. Percentage mortality and percentage of the larvae showing normal development in the F-2 instar of *Xanthocnemis zealandica* from Lake Sarah - tb, maintained at SD 20°C.

The number of larvae set up and the number responding (in brackets) in each experiment is indicated above the respective collection date.

Symbols:

circle	-	normal development
square	-	mortality
hollow	-	LD photoperiod
solid	-	SD photoperiod

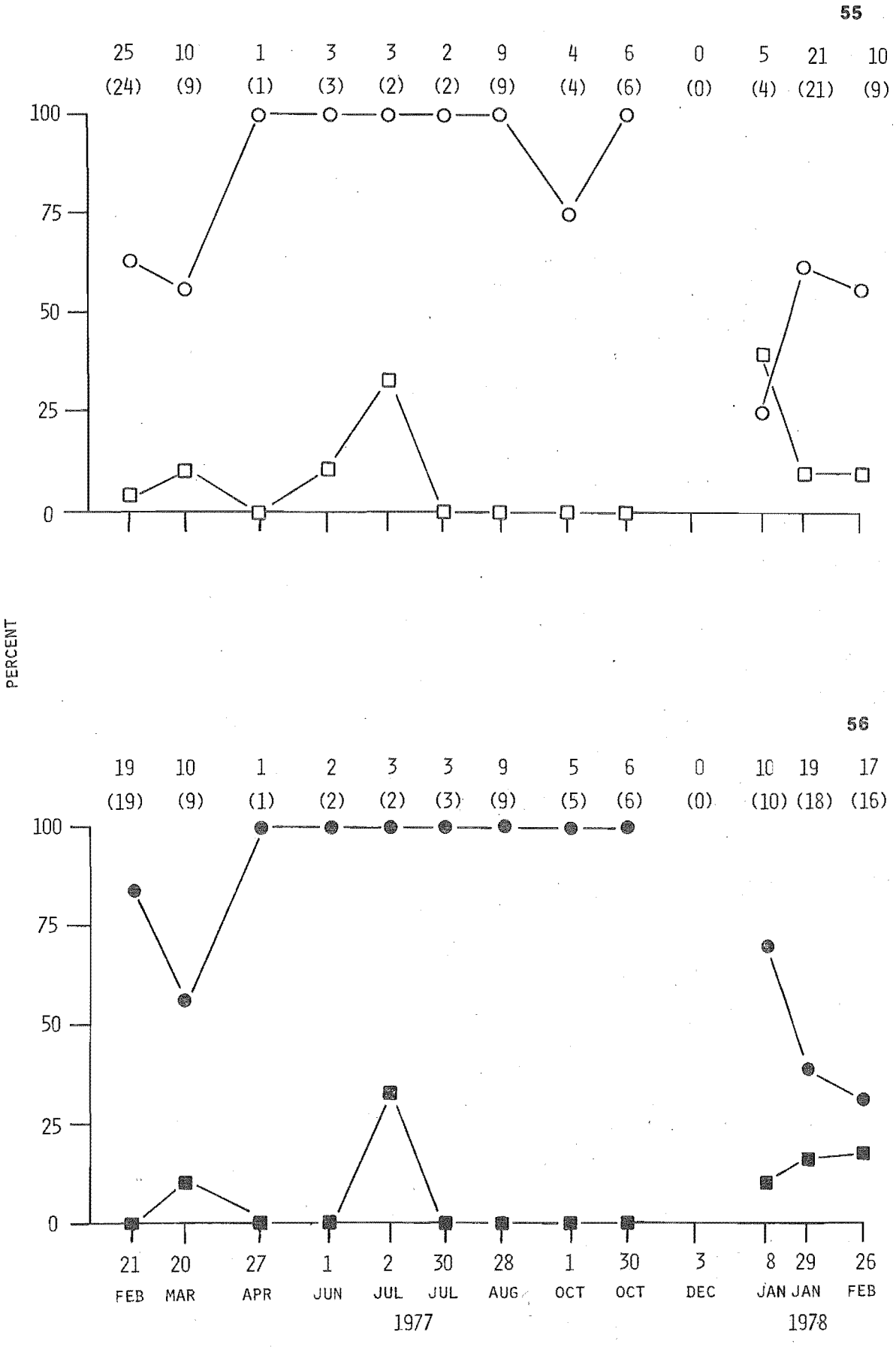

55
25 10 1 3 3 2 9 4 6 0 5 21 10
(24) (9) (1) (3) (2) (2) (9) (4) (6) (0) (4) (21) (9)
100
75
50
25
0
PERCENT
56
19 10 1 2 3 3 9 5 6 0 10 19 17
(19) (9) (1) (2) (2) (3) (9) (5) (6) (0) (10) (18) (16)
100
75
50
25
0
21 FEB
20 MAR
27 APR
1 JUN
2 JUL
30 JUL
28 AUG
1 OCT
30 OCT
3 DEC
8 JAN
29 JAN
26 FEB
1977
1978

Fig. 57. The mean duration (days) from collection to completion of the F-2 stadium of *Xanthocnemis zealandica* larvae from Lake Sarah - tb (± one standard deviation shown).

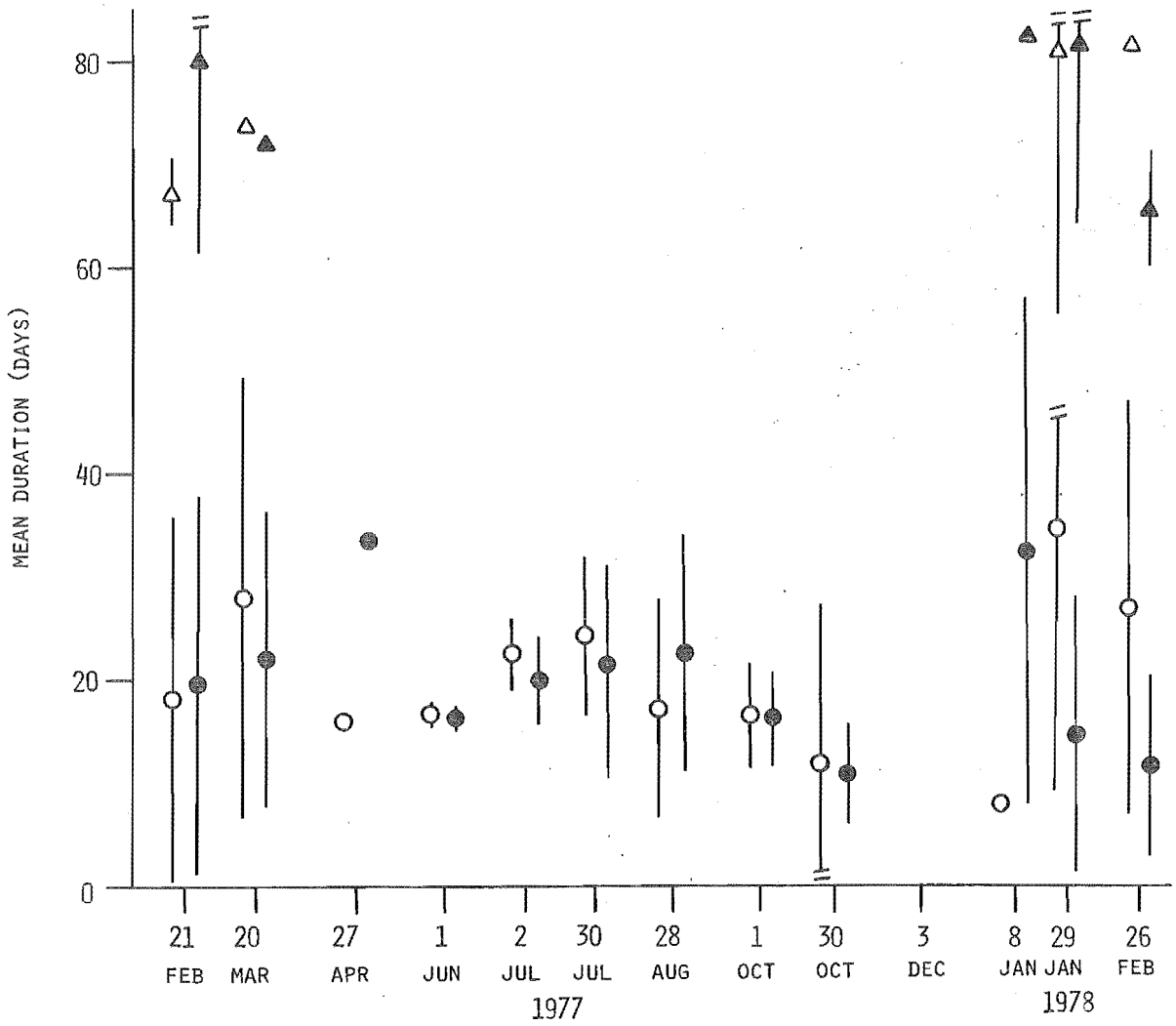
Symbols:

circle - normal development

triangle - prolonged development

hollow - LD 20°C

solid - SD 20°C


MEAN DURATION (DAYS)
0
20
40
60
80
21 FEB
20 MAR
27 APR
1 JUN
2 JUL
30 JUL
28 AUG
1 OCT
30 OCT
3 DEC
8 JAN
29 JAN
26 FEB
1977
1978

F-1 instar Larvae in the 1977 cohort were last collected on 8 January 1978 (Fig. 58). Only one larva was found and it was set up at the LD photoperiod which was close to the natural photoperiod at that time (16h 20min light). This was done to obtain an indication of the larval response to photoperiods prevalent in the field. Larvae in the 1978 cohort were first collected on 29 January 1978. The percentage mortality and the percentage of the larvae showing normal development, based on X_{max}, is presented in Figs. 58 & 59 for the LD and SD photoperiods, respectively.

Mortality was noticeable during two periods:

- from 21 February to approximately 30 July 1977; and
- from 29 January to 26 February 1978 (Figs. 58 & 59).

However, in the experiments from approximately 30 July 1977 to 8 January 1978, mortality was low.

No larvae in the LD photoperiod, collected on 21 February 1977, developed at the normal rate (Fig. 58), whereas from 27 April 1977 to 8 January 1978 almost all the larvae developed normally. One larva in the SD photoperiod (n = 14), collected on 21 February, developed at the normal rate (Fig. 59); however, it was not until 30 July that all the larvae developed normally. No larvae in the 1978 cohort, collected on 29 January 1978, developed at the normal rate in either photoperiod. By 26 February about 10% of the larvae developed at the normal rate in both the LD and SD conditions.

The mean duration for development in the F-1 instar normal development group (Fig. 60) was similar at both photoperiods for a given date from 20 March to 3 December 1977. The mean decreased slowly during the period from 27 April to 1 October, from about 30 to 20 days, respectively; then it decreased markedly by 30 October to about 10 days.

The F-1 instar larvae in the normal development group, collected on 26 February 1978, showed a differential response to the LD and SD photoperiods (Fig. 60) which was probably related to small sample size (n = 2).

The mean duration for development in the F-1 instar prolonged development group (Fig. 60), collected on 21 February and 20 March 1977, and on 26 February 1978, was longer in the LD, than in the SD photoperiod, whereas larvae collected on 29 January 1978 took longer to develop in the SD, than in the LD photoperiod. Larvae in the

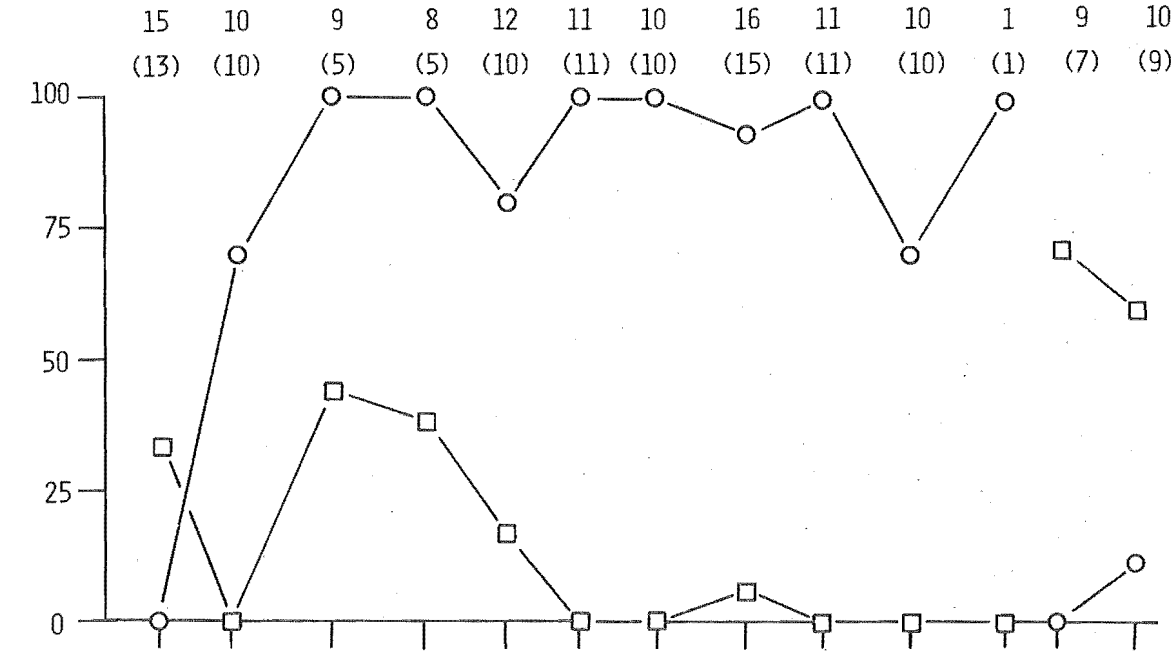
Fig. 58. Percentage mortality and percentage of the larvae showing normal development in the F-1 instar of *Xanthocnemis zealandica* from Lake Sarah - tb, maintained at LD 20°C.

Fig. 59. Percentage mortality and percentage of the larvae showing normal development in the F-1 instar of *Xanthocnemis zealandica* from Lake Sarah - tb, maintained at SD 20°C.

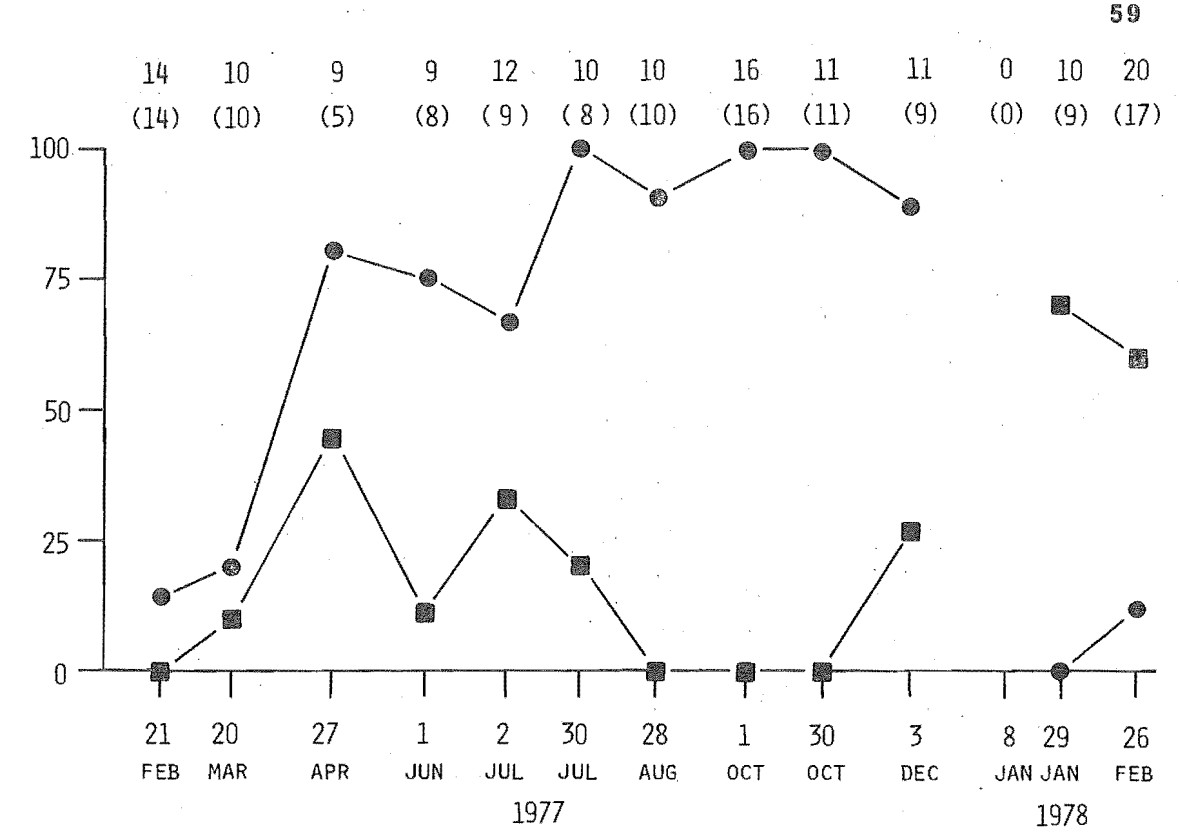
The number of larvae set up and the number responding (in brackets) in each experiment is indicated above the respective collection date.

Symbols:

circle	-	normal development
square	-	mortality
hollow	-	LD photoperiod
solid	-	SD photoperiod.


15 10 9 8 12 11 10 16 11 10 1 9 10
(13) (10) (5) (5) (10) (11) (10) (15) (11) (10) (1) (7) (9)
100
75
50
25
0

PERCENT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(14) (10) (5) (8) (9) (8) (10) (16) (11) (9) (0) (9) (17)
100
75
50
25
0
21 FEB
20 MAR
27 APR
1 JUN
2 JUL
30 JUL
28 AUG
1 OCT
30 OCT
3 DEC
8 JAN
29 JAN
26 FEB
1977
1978

Fig. 60. The mean duration (days) from collection to completion of the F-1 stadium of *Xanthocnemis zealandica* larvae from Lake Sarah - tb (± one standard deviation shown).

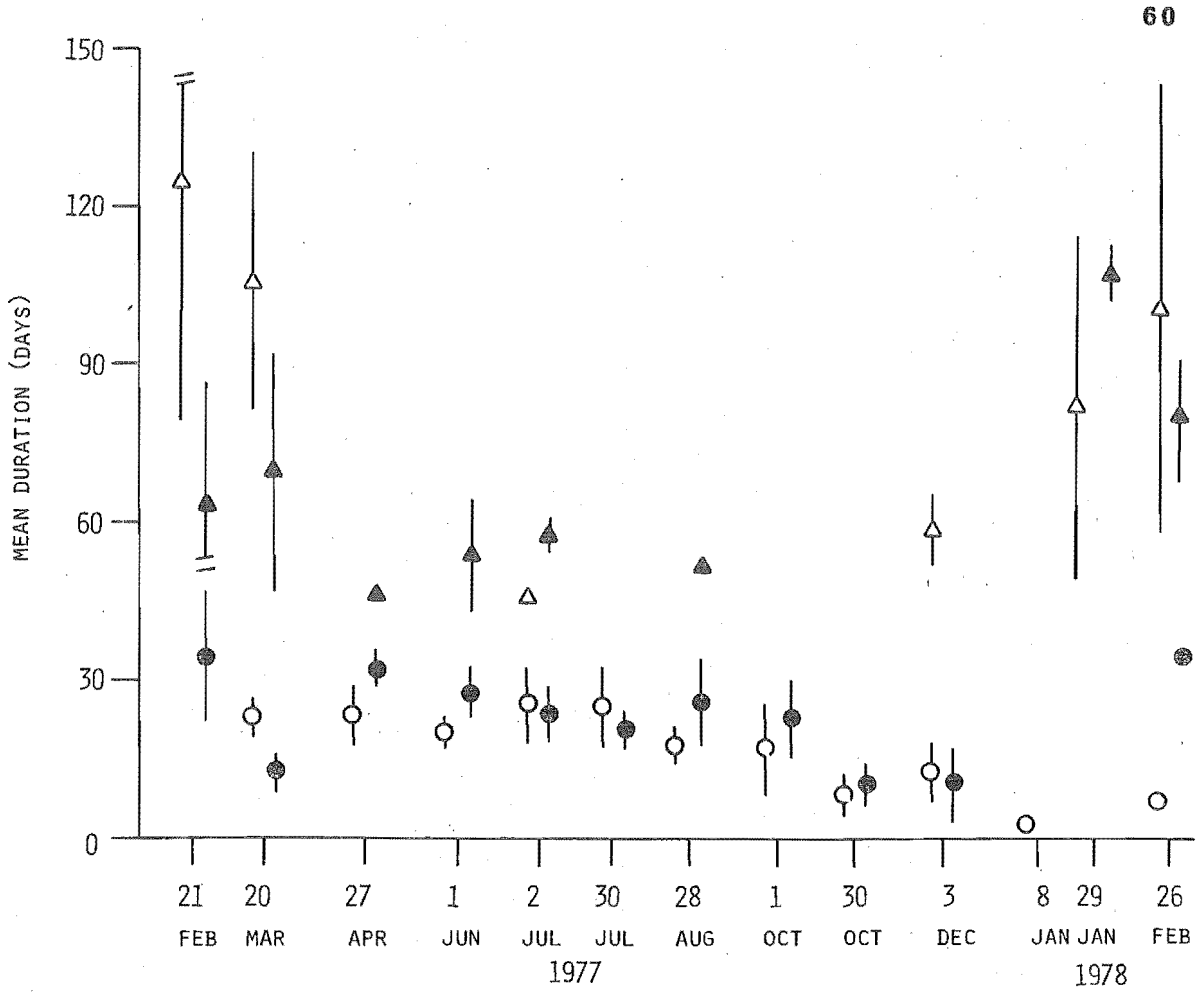
Symbols:

circle - normal development

triangle - prolonged development

hollow - LD 20°C

solid - SD 20°C.


MEAN DURATION (DAYS)
150
120
90
60
30
0
21 FEB
20 MAR
27 APR
1 JUN
2 JUL
30 JUL
28 AUG
1 OCT
30 OCT
3 DEC
8 JAN
29 JAN
26 FEB
1977
1978

prolonged development group that were collected between April and December completed development in less time (mean duration 50 to 60 days), than larvae collected between January and March (mean duration 60 to 120 days).

F instar up to early metamorphosis Larvae in the 1977 cohort were first collected on 20 March 1977 and last collected on 29 January 1978 (Fig. 61). Only two larvae were found on this latter date and they were both set up at the LD photoperiod which was relatively close to the natural photoperiod (15h 36min light) experienced in the field at this time. No larvae in the 1978 cohort had appeared by 26 February 1978. The percentage mortality and the percentage of the larvae showing normal development, based on X_{max} up to early metamorphosis, is presented in Figs. 61 & 62 for the LD and SD photoperiods, respectively.

Mortality was noticeable from approximately 20 March to approximately 30 July 1977 (Figs. 61 & 62), whereas mortality was low in the experiments from approximately 30 July 1977 to 29 January 1978.

No larvae in the LD photoperiod, collected on 20 March or 27 April 1977, developed at the normal rate (Fig. 61) and it was not until 1 October 1977 that all or almost all of the larvae in the collection developed normally. No larvae in the SD photoperiod, collected on 20 March 1977 developed at the normal rate. Some larvae developed normally by 27 April but it was not until 30 October 1977 that all or almost all of the larvae developed at this rate.

The mean duration for development up to early metamorphosis in the F instar normal development group (Fig. 63) was similar at both photoperiods for a given date. The mean duration for development remained at approximately 17 to 20 days from April to late August, then decreased to 12.5 days by 1 October, and 5.0 to 8.0 days by 30 October 1977. It increased to 10 to 15 days, 3 December 1977, but again decreased during January 1978 until all the larvae were in metamorphosis when collected on 29 January 1978.

The mean duration for development up to early metamorphosis in the F instar prolonged development group when collected on 20 March 1977 (Fig. 63) was 58 days at the SD photoperiod, but 33 days at the LD photoperiod. Thereafter, the mean duration was similar at both photoperiods (25 to 30 days).

F instar 'metamorphosis' During the above experiments with the F instar larvae observations were also made on the time required for the

Fig. 61. Percentage mortality and percentage of the larvae showing normal development in the F instar of *Xanthocnemis zealandica* from Lake Sarah - tb, maintained at LD 20°C.

Fig. 62. Percentage mortality and percentage of the larvae showing normal development in the F instar of *Xanthocnemis zealandica* from Lake Sarah - tb, maintained at SD 20°C.

The number of larvae set up and the number responding (in brackets) in each experiment is indicated above the respective collection date.

Symbols:

circle - normal development

square - mortality

hollow - LD photoperiod

solid - SD photoperiod.

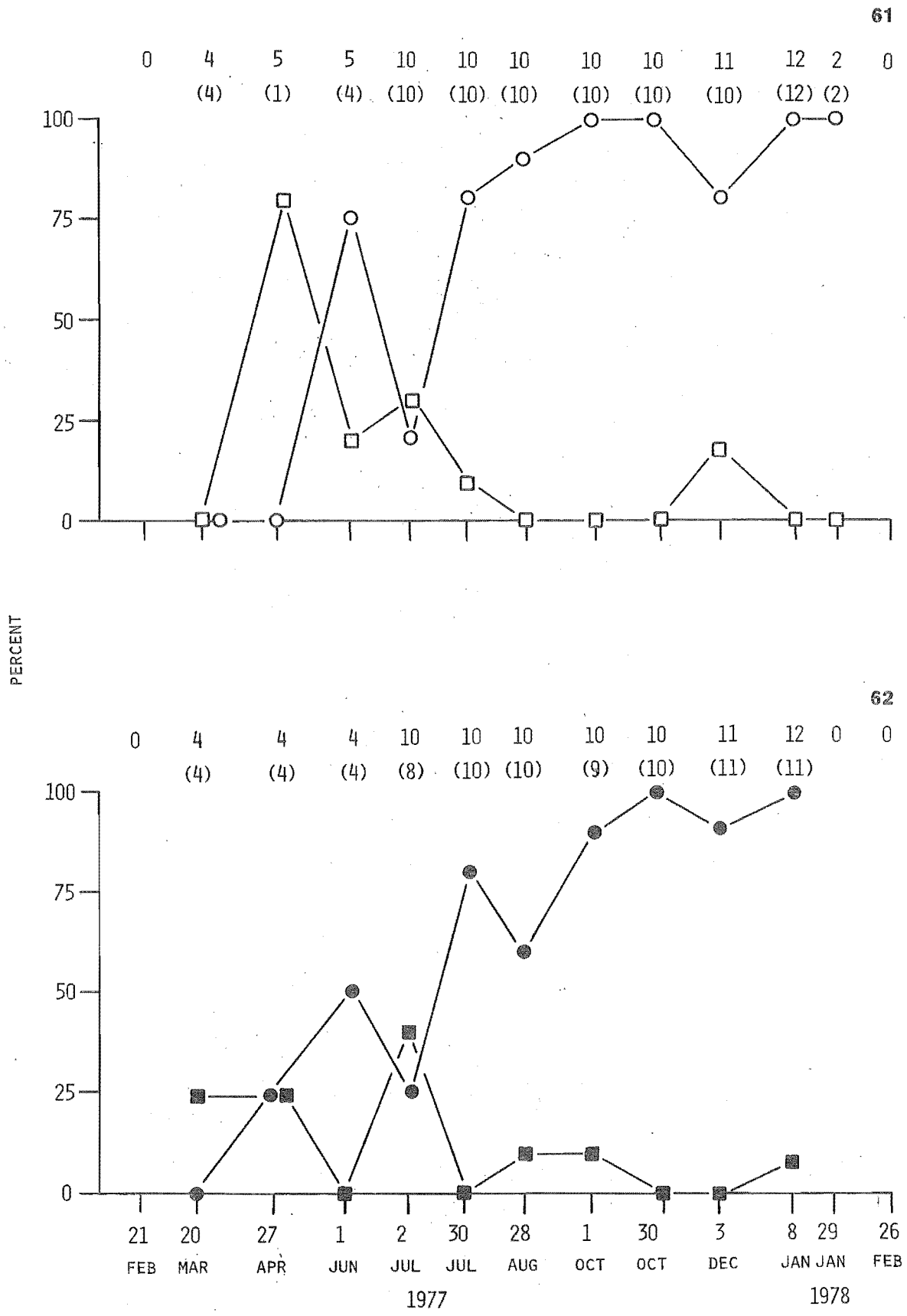
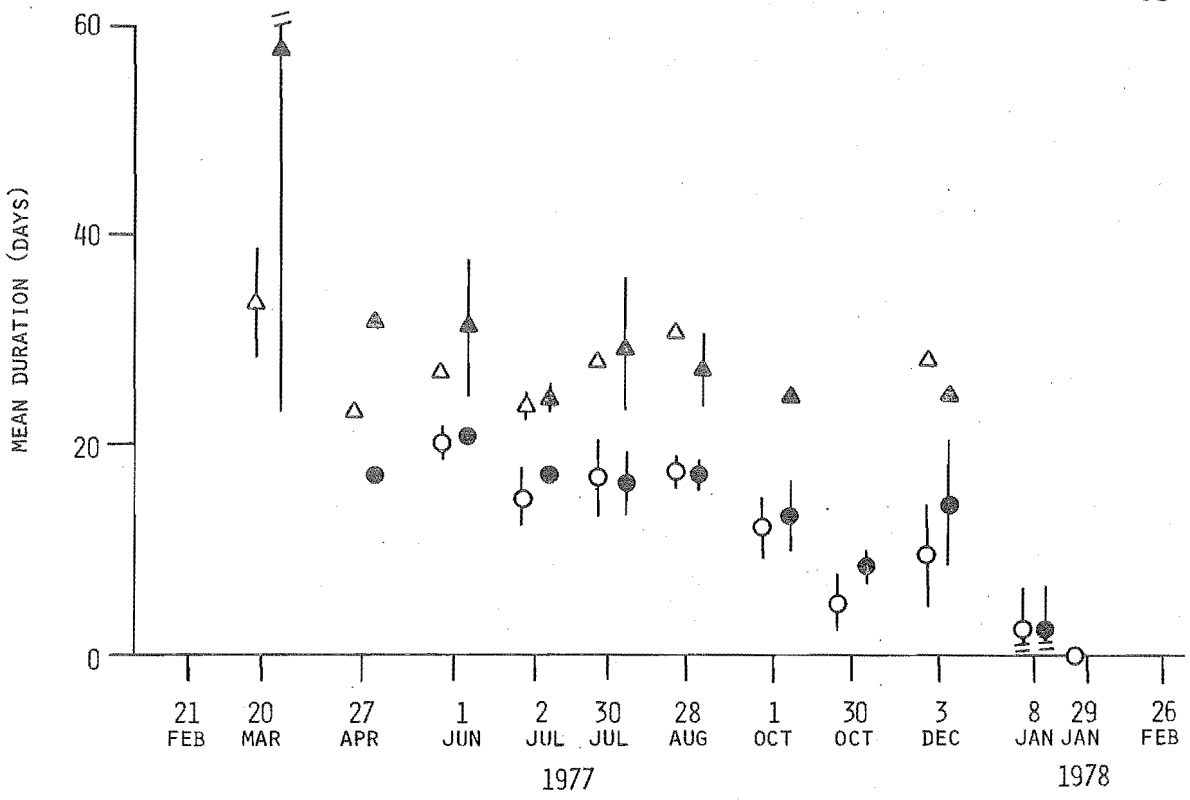

61
0 4 5 5 10 10 10 10 10 11 12 2 0
(4) (1) (4) (10) (10) (10) (10) (10) (10) (12) (2)
100
75
50
25
0
PERCENT
62
0 4 4 4 10 10 10 10 10 11 12 0 0
(4) (4) (4) (8) (10) (10) (9) (10) (11) (11)
100
75
50
25
0
21 FEB
20 MAR
27 APR
1 JUN
2 JUL
30 JUL
28 AUG
1 OCT
30 OCT
3 DEC
8 JAN
29 JAN
26 FEB
1977
1978

Fig. 63. The mean duration (days) from collection to completion of the F stadium (up to early metamorphosis) of *Xanthocnemis zealandica* larvae from Lake Sarah - tb (± one standard deviation shown).

Symbols:

circle	-	normal development
triangle	-	prolonged development
hollow	-	LD 20°C
solid	-	SD 20°C.


MEAN DURATION (DAYS)
60
40
20
0
21 FEB
20 MAR
27 APR
1 JUN
2 JUL
30 JUL
28 AUG
1 OCT
30 OCT
3 DEC
8 JAN
29 JAN
26 FEB
1977
1978

completion of development from early metamorphosis to emergence. The results indicated that no larvae required longer than X_{max} (13 days) to complete development in the laboratory. The rate of development was similar at both photoperiods and varied only slightly during the year, with no apparent seasonal trend. For these reasons detailed studies concerning possible seasonal changes in the duration of this metamorphosis stage and further analyses of the results were considered unnecessary.

7.3.3.2. Comments - Lake Sarah - tb The mortality trends and the changes in the mean duration for development in the normal development groups are discussed in a general fashion for the various stages tested. The use of the X_{max} value to distinguish the larvae in the population that developed at the normal or prolonged rates is then examined, after which development and response of larvae to photoperiod during the year is discussed instar by instar.

The mortality experienced by the *X. zealandica* larvae from Lake Sarah - tb during these experiments appeared to be seasonal (Figs. 55, 56, 58, 59, 61 & 62). Generally, mortality was low during the spring to summer months when a large proportion of the population developed at the normal rate, for example see 30 July 1977 to 8 January 1978, Fig. 61. Conversely, mortality was high during the period when a small proportion of the population developed at the normal rate, *i.e.* when larvae developed at a prolonged (non-normal) rate. Examples of this situation occurred on 29 January and 26 February 1978, Fig. 58. This high mortality was probably related to stress experienced by the larvae in the prolonged development group, caused by the constant photoperiod and temperature regimens in the laboratory. Ingram (1976a) found that *E. aspersum* and *E. hageni* when kept at 11 L:13 D and 21°C experienced high mortality. He attributed this to prolonged exposure of the larvae to contrasting developmental signals, *i.e.* an inhibitory photoperiod combined with a temperature promoting growth, a situation believed to be similar to the one observed here. *X. zealandica* larvae required the changing field conditions (photoperiod and/or temperature) to promote a rapid change to the normal development rate. The constant laboratory regimens maintained larvae in a state of prolonged development at a relatively high temperature (20°C), which probably caused the high mortality experienced.

High mortality was also noted during the winter (for example, see 2 July 1977, Fig. 55), perhaps because of the shock associated with the sudden change from 4°C conditions in the field to 20°C conditions in the laboratory.

The changes in the mean duration for development in the normal development groups were believed to reflect the periods of larval growth in the field. Shepard & Lutz (1976) found that the mean duration for development of the F instar larvae of *Plathemis lydia* Drury decreased during the autumn but remained similar during the mid-winter period, which indicated that little physiological maturation occurred during the winter months. With the onset of spring the mean duration for development again decreased; however, it increased in the final collection made during May, which probably indicated renewed recruitment into the F instar. The F instar group during May showed a wider variation in physiological maturity than in the previous collections; consequently the mean duration for development increased.

Generally in the present study, little development of *X. zealandica* larvae in the F-2 instar or the F instar up to early metamorphosis occurred during the winter collections, 1 June to 28 August 1977, (Figs. 57 & 63) at Lake Sarah - tb. An exception to this was the slight decrease in the mean duration for development of the F-1 instar larvae during the same period (Fig. 60). This indicated that the threshold temperature for development was sufficiently low to permit development of larvae in the F-1 instar during the winter when the mean water temperature was about 4°C and the maximum was 7°C. This supported the observation that the threshold temperature for development of F-1 instar larvae was lower than those of the other stages examined in section 7.3.1. (Table 22). The exact threshold temperature of the F-1 instar larvae is unknown; however, as discussed earlier (section 7.3.1.), it is probably higher than the calculated value of 3.8°C but lower than 7°C, the maximum water temperature that was recorded in the field during this period.

Between 28 August and 1 October 1977 the maximum water temperature rose to 10°C which was above the threshold temperatures calculated for the remaining instars studied (Table 22). Consequently mean duration for development of each of the instars decreased by 1 October and decreased markedly between 1 and 30 October 1977 (Figs. 57, 60 & 63). The mean water temperature was 9.1°C and the maximum 15°C during October 1977. Development in the field started

between 28 August and 1 October in 1977 and rapid development occurred during October. The larval survey showed that a noticeable mean head width increase occurred in cohort 1 during October-November 1976 (Fig. 18). The results here showed that rapid development occurred during October 1978 and was probably followed by a sharp burst of moulting at the end of October or during November. This may indicate that each year the growth season at Lake Sarah - tb starts during October.

The increase in the mean duration and standard deviation for development of F instar larvae up to early metamorphosis in the normal development group that occurred by 3 December (Fig. 63) was believed to indicate recruitment into the F instar from earlier instar larvae. For example, the moulting of F-1 instar larvae into the F instar population during November would result in a greater diversity of ages. Consequently the mean duration and standard deviation for development of the F instar group would increase. This was believed to be similar to the response that Shepard & Lutz (1976) observed in *P. lydia* F instar larvae collected during the late spring (May).

The decrease of the mean duration for development of the F instar larvae of *X. zealandica* by 8 January 1978 indicated a reduction or cessation of recruitment into the F instar. By 29 January the only individuals left in the F instar population were in metamorphosis which confirmed that recruitment into the F instar ended some time during early January. A similar pattern was observed in the F-1 instar normal development group (Fig. 60). A slight increase in the mean duration for development occurred by 3 December 1977, followed by a decrease in the mean by 8 January 1978. These observations supported the earlier suggestion that a burst of moulting probably took place after 30 October 1977, as indicated by the increased means of 3 December 1977. These observations also suggested that the end of the period of recruitment into the F and F-1 instars was December, as indicated by the greatly reduced means in the collection(s) of 8 and 29 January 1978 (F instar) or of 8 January 1978 (F-1 instar).

As mentioned earlier (p.130) the larvae in these experiments were of an unknown age, *i.e.* at the time of collection the larvae had already spent an unknown amount of time in the particular instar in which they were collected. Therefore, the period for the completion

of development that was observed in the laboratory represented a minimum value for the stadium in question. This resulted in a possible over-estimate of the proportion of the population of larvae showing normal development for a given date.

Despite these problems a recurring seasonal pattern of prolonged development was evident for each of the stages tested. Based on the X_{max} values, a larger percentage of the population than expected ($P<0.05$) developed at the prolonged rates in each instar, mainly during the period from January to March-April. For examples of this recurring pattern see February 1977 and 1978 for the F-2 and F-1 instars (Figs. 55 & 56 and 58 & 59, respectively). Further to this, larvae in the prolonged development group occasionally took well above the X_{max} value to complete development. For example, F-1 instar larvae with an X_{max} of 44 days often required more than 100 days and one required 198 days to complete development in the prolonged development group during January, February and March. Also, although the X_{max} value for F-2 instar larvae (63 days) was believed to be an over-estimate (section 7.3.1.2.) some larvae in the prolonged development group still required up to 112 days to complete development during the period January to March.

These two trends, the recurring seasonal pattern of prolonged development and the long period required for development by the larvae (up to two or three times the X_{max} value), were believed to confirm the existence of two rates of development in the larval population. The X_{max} values, calculated for each of the stages tested, served adequately to distinguish the larvae in the population that developed at the normal or prolonged rates.

Results indicated that, unlike the F-1 and F instar larvae, some F-2 instar larvae developed at the normal rate during the entire year (Figs. 55 & 56). Initially this was believed to be an artifact caused by the over-estimated X_{max} value; however, close inspection of the results showed that in each experiment some larvae completed development within ten days, a value considered to be indicative of normal development. Therefore, the seasonal pattern of development obtained for the F-2 instar larvae probably reflected the response of the larvae in the field, *i.e.* that some larvae developed at the normal rate during the entire year. This pattern was not observed in the F-1 and F instar larvae. During February or March all the larvae in these instars developed at the prolonged rate in the LD photoperiod (Figs. 58 & 61).

Now that the prolonged development of the larvae has been confirmed as a valid observation the seasonal development and response of the larvae to photoperiod can be discussed. The factors that were considered likely to affect the responses of larvae undergoing prolonged development were:

- exposure to falling or cool temperatures; and
- exposure to the photoperiods experienced during the autumnal equinox.

Corbet (1956a) discussed the relationship between exposure to cold and the completion of diapause in *Anax imperator* Leach larvae and Ingram (1975) demonstrated that pretreatment at 10°C of *E. hageni* and *E. aspersum* larvae in diapause stimulated subsequent development at 14L:10D and 21°C conditions. Lutz (1974a, 1974b) demonstrated that the photoperiods during the autumnal equinox influenced the development of *T. cynosura* larvae. A photoperiod of 14L:10D prolonged development before the autumnal equinox, whereas shortly after the equinox the same photoperiod promoted rapid development.

In the present study special attention was paid to:

- the period during which prolonged development occurred;
- the timing of the change to normal development; and
- the intensity of the response at the different photoperiods during the year.

Within a given instar the larvae in the prolonged development group apparently could show a strong or a weak response. For example, F-1 instar larvae took a mean of more than 100 days to complete development in the LD photoperiod during February and March 1977 (Fig. 60), whereas they took a mean of approximately 55 days to complete development in the SD photoperiod during June 1977. In this example the former is considered a strong response, whereas the latter is considered a weak one.

Seasonal development and response of the larvae to photoperiod is examined only briefly at this stage. Implications are suggested, but the final discussion of their significance is left for section 7.3.4., when the results from the Lake Sarah - tb (sections 7.3.3.1. & 7.3.3.2.) and Isaac's Pond (sections 7.3.3.3. & 7.3.3.4.) larval studies are available for comment.

F-2 instar Prolonged development in the F-2 instar larvae at Lake Sarah - tb was evident 8 January 1978 (Figs 55 & 56) at the time of the appearance of this instar in the new cohort. The mean

water temperature was relatively stable during December to February, about 15°C (Fig. 13); therefore, the induction of prolonged development was probably cued by photoperiod.

All the larvae tested changed to development at the normal rate by 27 April 1977 (Figs. 55 & 56). Between 20 March and 27 April the water temperature fell noticeably and the autumnal equinox occurred. Either of these factors or perhaps a combination of both may have been responsible for this change in the rate of development.

The proportion of the F-2 instar larval population in the prolonged development group was high in the LD photoperiod during January 1978 but decreased by late February (Fig. 55), whereas the proportion was low in the SD photoperiod during January but increased by February (Fig. 56). This initial differential response to the two photoperiods indicated that the larvae were sensitive to photoperiod; therefore, the prolonged development response was facultative, *i.e.* it was more readily manifested in the population when certain environmental conditions occurred at critical times during the year. The larvae in the field probably responded primarily to photoperiod, rather than primarily to temperature. As mentioned earlier, the water temperature was relatively stable during January and February 1978.

By late February and during March 1977 the proportion of the larvae in the prolonged group was similar in both photoperiods. The larvae were now insensitive to photoperiod, possibly because of the effect of falling temperature and/or the changing photoperiod experienced in the field.

The intensity of the prolonged development response (approximate mean duration 70 to 80 days) was similar at either photoperiod. Apparently the day length in the laboratory had little effect on the intensity of prolonged development; or what is more likely, the over-estimated X_{max} value may have reduced fluctuations of the mean by screening responses close to but less than the X_{max} value (63 days). The latter situation was believed to cause the differential response to photoperiod that was displayed briefly by larvae in the normal development group during January 1978 (Fig. 57). This also caused the larger standard deviations calculated for the larvae in the SD photoperiod 8 January and in the LD photoperiod 29 January (Fig. 57). A better estimate of X_{max} could resolve this question; however, the results still indicated prolonged development at both photoperiods in the laboratory during this period.

Results from the larval survey (section 4.3.2.) indicated that a possible growth restriction occurred in the F-3 and/or F-2 instar larvae during November and December at Lake Sarah - tb. During this period in 1977 no F-2 instar larvae were collected; however, some F-3 instar larvae were found. Although no formal experiments were carried out using F-3 instar larvae, the few observations that were made, 3 December 1977, indicated supplementary moulting and possibly, prolonged development in some larvae. These results and those for the F-2 instar that were discussed earlier supported the inferences made in section 4.3.2. . A possible growth restriction in the F-3 instar larvae was suggested and a growth restriction in the F-2 instar larvae was confirmed.

F-1 instar Prolonged development in the F-1 instar larvae at Lake Sarah - tb was evident 29 January 1978 (Figs. 58 & 59) at the time of the appearance of this instar in the new cohort. As in the F-2 instar, temperature was not considered to be the predominant (over-riding) environmental cue. The induction of prolonged development was probably cued by photoperiod.

Larvae in the LD photoperiod (Fig. 58) changed to development at the normal rate by 27 April 1977 which was the same timing as observed in the F-2 instar, probably for the same reasons. The F-1 instar larvae in the SD photoperiod changed to development at the normal rate after late July (Fig. 59). The cool conditions that the larvae experienced in the field from May to July (Fig. 13) may have caused this change to the normal rate of development, *i.e.* larvae became insensitive to photoperiod and developed at the same rate in the LD or SD conditions.

The proportion of the F-1 instar larval population in the prolonged development group was initially similar (almost 100%) at both photoperiods (see February 1977 and January & February 1978, Figs. 58 & 59), but became increasingly dissimilar thereafter, as discussed above. This seasonal sensitivity to photoperiod indicated that prolonged development was facultative.

The intensity of the prolonged development response was dissimilar at the two photoperiods (Fig. 60). A strong response (mean duration approximately 100 to 120 days) was exhibited by F-1 instar larvae in the SD photoperiod during January 1978 and in the LD photoperiod during February & March 1977 and February 1978. The response was weaker (mean duration 60 to 70 days) in the SD photoperiod during February and March 1977 and after the autumnal equinox larvae in the prolonged development group consistently showed a weak response

(mean duration 50 to 60 days). Apparently the larvae in the LD photoperiod developed at the normal rate after exposure to cold and/or equinoctial photoperiods, whereas larvae in the SD photoperiod showed a progressive decrease in the intensity of the prolonged development response from late January. This intensity change, that occurred during January-February in the LD photoperiod, was probably cued by photoperiod in the field because temperatures were relatively constant at that time (Fig. 13).

After April larvae occasionally showed a weak prolonged response in both photoperiods (Fig. 60) without an apparent pattern. Perhaps the weak response reflects a minor developmental restriction experienced by individual larvae dependent on previous exposure, whereas the strong response reflects a major developmental restriction experienced by the entire population that occurs from January to March only (see p.171).

The larval survey (section 4.3.2.) failed to detect a growth restriction in the F-1 instar larvae at Lake Sarah - tb; however, at Isaac's Pond (section 4.3.1.) a growth restriction was evident in this instar. The above observations indicate that a growth restriction also occurs in the F-1 instar larvae at Lake Sarah - tb.

F instar up to early metamorphosis Prolonged development in the F instar at Lake Sarah - tb was first evident 20 March 1977 (Figs. 61 & 62) at the time of the appearance of this instar in the new cohort. The induction of prolonged development was probably cued by photoperiod, although falling temperatures, as experienced in the field at Lake Sarah - tb during March (Fig. 13), may have interacted with photoperiod to affect the rate of development.

The larvae slowly changed to development at the normal rate during the period from March to October (Figs. 61 & 62). This change appeared to be elicited by exposure to cool conditions in the field, but the change occurred at a regular rate, without a distinct transition period; therefore other factors may have been involved also.

The proportion of the larvae that developed at the prolonged rate at both photoperiods in the laboratory was similar for a given date, which indicated that the larvae were insensitive to photoperiod. However, the intensity of the prolonged development response on 20 March 1977 (Fig. 63) was dissimilar in the two photoperiods. A strong response (mean duration 55 days) was exhibited in the SD photoperiod on 20 March, whereas a weak response (mean duration

approximately 30 days) was always obtained in the LD photoperiod, and in the SD photoperiod after March. These differences in the intensity of the prolonged development response indicated that the response was facultative and that larvae lost their sensitivity to photoperiod at the time of the autumnal equinox. Therefore, the equinoctial photoperiods and/or falling temperatures may have cued the end of the strong response, whereas exposure to cool conditions terminated the weak response.

Larvae in the F instar occasionally showed a weak prolonged development response after the change to normal development apparently was completed (*i.e.*, approximately October). This was also observed in the F-1 instar larvae. Perhaps this weak response, as suggested earlier (see *F-1 instar*) reflects a minor developmental restriction experienced by individual larvae, whereas the strong response reflects a major developmental restriction experienced by the entire population (see p.171).

The larval survey (section 4.3.3.) indicated a possible growth restriction in F instar larvae at Lake Sarah - tb that occurred during March. This suggestion was confirmed by the above results.

F instar 'metamorphosis' Larvae that started metamorphosis continued development to emergence at a rate that appeared dependent on temperature only. After larvae started metamorphosis no response to photoperiod was detected nor was a seasonal change of response evident. The growth restrictions that occurred in earlier instar larvae ensured that metamorphosis started at a time of the year when emergence, maturation of the adult and reproduction was possible.

7.3.3.3. Results - Isaac's Pond F-2 instar Larvae in the 1977 cohort were last collected on 30 December 1977 (Figs. 64 & 65). Larvae in the 1978 cohort were first collected 3 February 1978 and set up at the LD photoperiod which was closest to the natural photoperiod (15h 14min) at that time. The percentage mortality and the percentage of the larvae showing normal development, based on X_{max}, is presented in Figs. 64 & 65 for the LD and SD photoperiods, respectively.

Pronounced mortality trends, common to larvae in both photoperiods, were not evident in these experiments (Figs. 64 & 65).

The larvae in the 1977 cohort all developed at the normal rate in both photoperiods (Figs. 64 & 65). Only about half of the larvae in the 1978 cohort developed at the normal rate during February and

Fig. 64. Percentage mortality and percentage of the larvae showing normal development in the F-2 instar of *Xanthocnemis zealandica* from Isaac's Pond, maintained at LD 20°C.

Fig. 65. Percentage mortality and percentage of the larvae showing normal development in the F-2 instar of *Xanthocnemis zealandica* from Isaac's Pond, maintained at SD 20°C.

The number of larvae set up and the number responding (in brackets) in each experiment is indicated above the respective collection date.

Symbols:

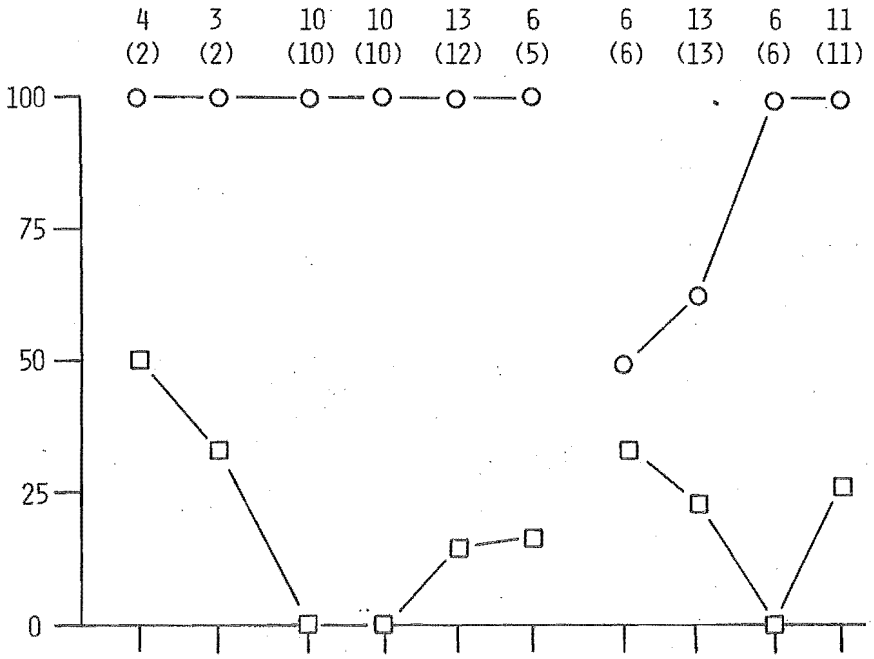
circle - normal development

square - mortality

hollow - LD photoperiod

solid - SD photoperiod

64



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65

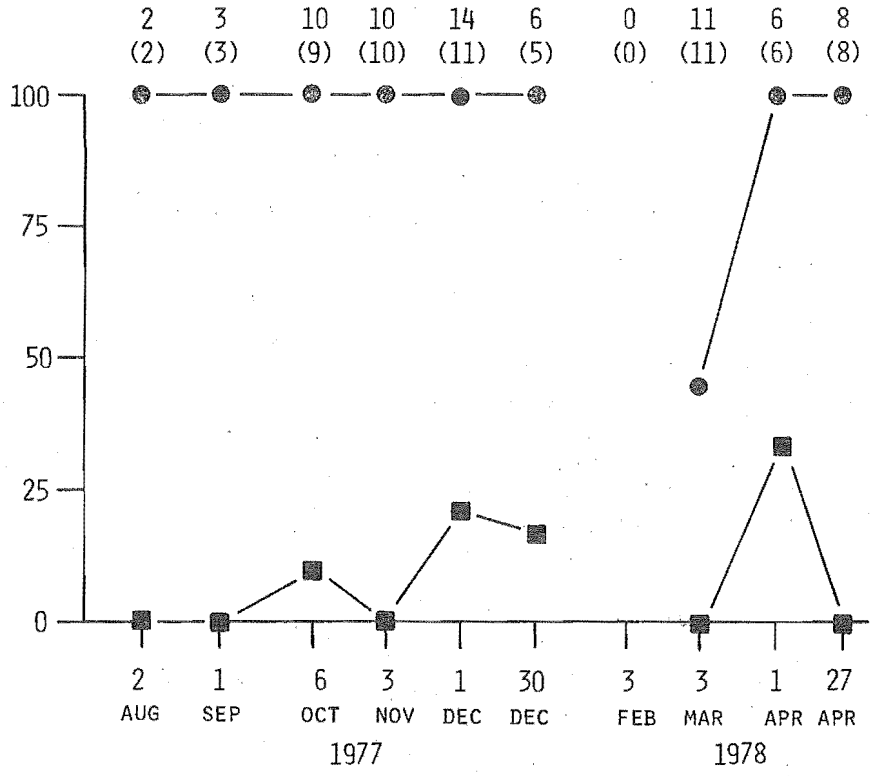


Fig. 66. The mean duration (days) from collection to completion of the F-2 stadium of *Xanthocnemis zealandica* larvae from Isaac's Pond (± one standard deviation shown).

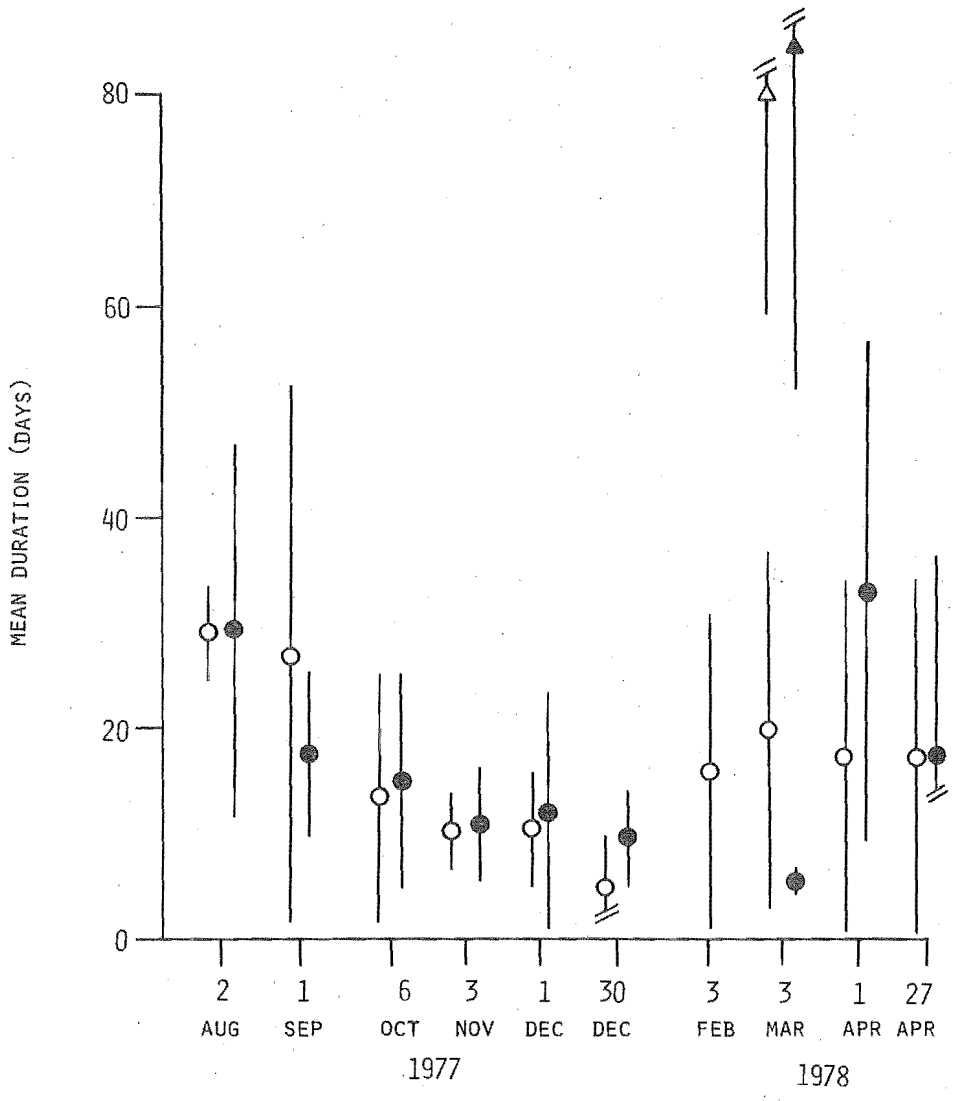
Symbols:

circle - normal development

triangle - prolonged development

hollow - LD 20°C

solid - SD 20°C.


MEAN DURATION (DAYS)
80
60
40
20
0
2 AUG
1 SEP
6 OCT
3 NOV
1 DEC
30 DEC
3 FEB
3 MAR
1 APR
27 APR
1977
1978

March but by 1 April all the larvae developed at this rate in both photoperiods.

The mean duration for development in the F-2 instar normal development group (Fig. 66) was similar at both photoperiods for a given date during this study, except for 3 March and 1 April 1978 which varied probably because of an over-estimated X_{max} value as discussed earlier (see p.150). The mean duration for development decreased markedly during the period from 2 August to 6 October and then slowly until 30 December.

The mean duration for development in the F-2 instar prolonged development group (Fig. 66) was similar at both photoperiods, about 80 to 85 days on 3 March 1978.

F-1 instar Larvae in the 1977 cohort were last collected on 30 December 1977 and did not appear in the 1978 cohort until the collection of 3 February 1978. The percentage mortality and the percentage of the larvae showing normal development, based on X_{max}, is presented in Figs. 67 & 68 for the LD and SD photoperiods, respectively.

Mortality varied during the period from August to December; however, it was consistently high in both photoperiods from March to late April (Figs. 67 & 68).

The larvae in the 1977 cohort all developed at the normal rate in both photoperiods (Figs. 67 & 68). About half of the larvae in the 1978 cohort developed at the normal rate in the LD photoperiod on 3 March (Fig. 67), whereas no larvae developed at this rate in the SD photoperiod (Fig. 68). By 27 April a similar proportion of the population developed at the normal rate in both photoperiods.

The mean duration for development in the F-1 instar normal development group (Fig. 69) was similar at both photoperiods for a given date during this study, except for 2 August 1977 which was probably related to small sample size (LD and SD combined n = 3) and 1 April 1978 which varied probably because of an over-estimated X_{max} value as discussed earlier for the F-2 instar larvae at Lake Sarah - tb (see p.150). The mean duration for development decreased slowly during the period from approximately 2 August to 30 December 1977.

The mean duration for development in the F-1 instar prolonged development group (Fig. 69) was greater in the SD photoperiod (60 to 70 days) than in the LD photoperiod (45 days) during April 1978.

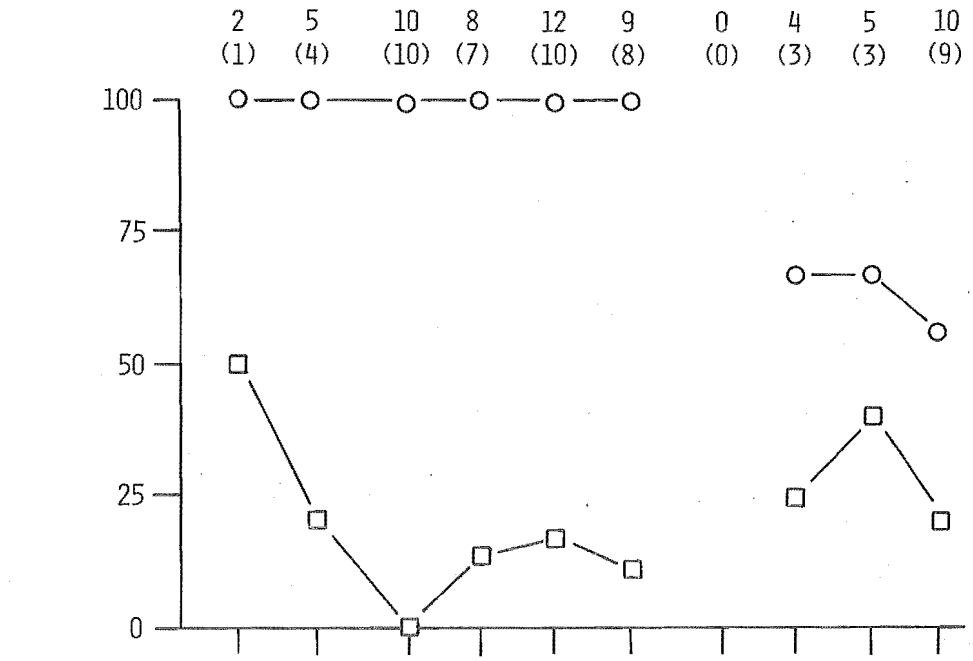
Fig. 67. Percentage mortality and percentage of the larvae showing normal development in the F-1 instar of *Xanthocnemis zealandica* from Isaac's Pond, maintained at LD 20°C.

Fig. 68. Percentage mortality and percentage of the larvae showing normal development in the F-1 instar of *Xanthocnemis zealandica* from Isaac's Pond, maintained at SD 20°C.

The number of larvae set up and the number responding (in brackets) in each experiment is indicated above the respective collection date.

Symbols:

circle	-	normal development
square	-	mortality
hollow	-	LD photoperiod
solid	-	SD photoperiod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(1) (4) (10) (7) (10) (8) (0) (3) (3) (9)
100
75
50
25
0

PERCENT

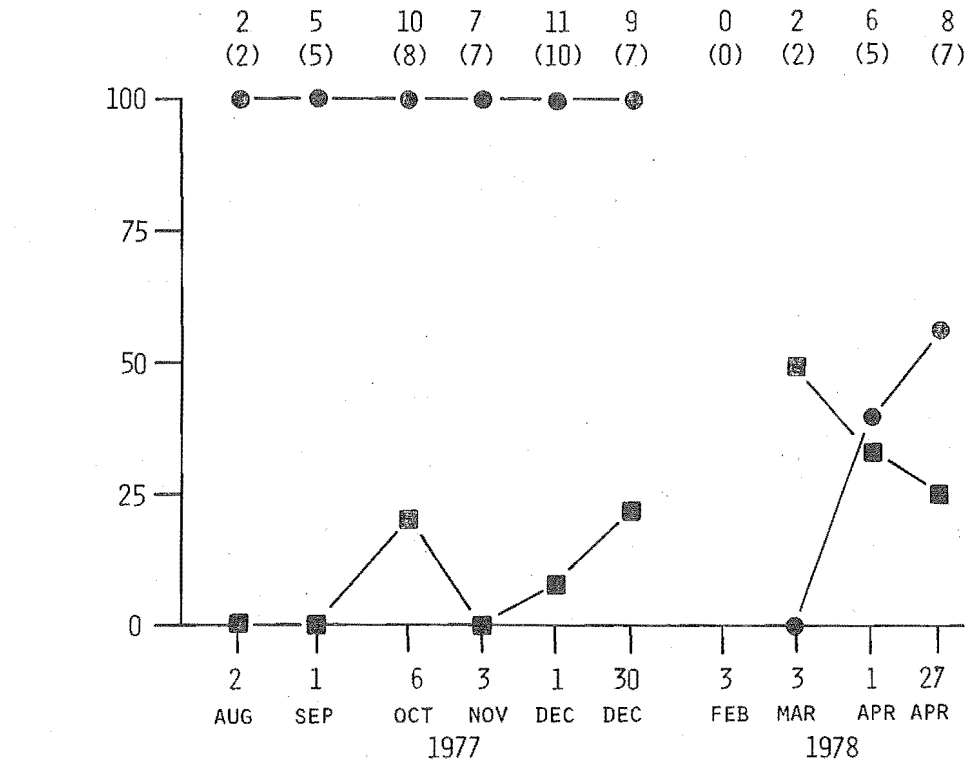

2 5 10 7 11 9 0 2 6 8
(2) (5) (8) (7) (10) (7) (0) (2) (5) (7)
100
75
50
25
0
2 1 6 3 1 30 3 3 1 27
AUG SEP OCT NOV DEC DEC FEB MAR APR APR
1977
1978

Fig. 69. The mean duration (days) from collection to completion of the F-1 stadium of *Xanthocnemis zealandica* larvae from Isaac's Pond (± one standard deviation shown).

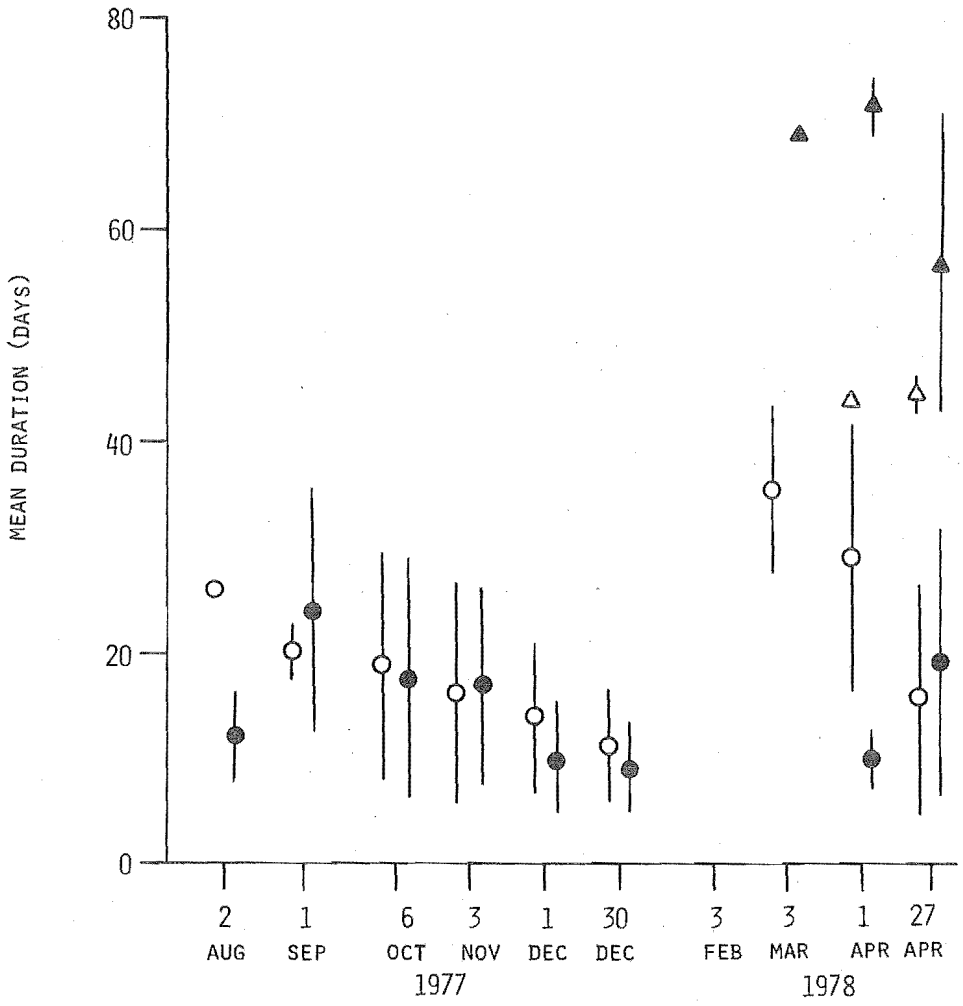
Symbols:

circle - normal development

triangle - prolonged development

hollow - LD 20°C

solid - SD 20°C.


MEAN DURATION (DAYS)
80
60
40
20
0
2 AUG
1 SEP
6 OCT
3 NOV
1 DEC
30 DEC
3 FEB
3 MAR
1 APR
27 APR
1977
1978

F instar up to early metamorphosis Larvae in the 1977 cohort were last collected on 3 February 1978 and did not appear in the 1978 cohort until 1 April. The percentage mortality and the percentage of the larvae showing normal development, based on X_{max}, is presented in Figs. 70 & 71 for the LD and SD photoperiods, respectively.

Pronounced mortality trends, common to larvae in both photoperiods, were not evident in these experiments (Figs. 70 & 71).

Three larvae (n = 4) developed at the normal rate on 2 August 1977 in both photoperiods (Figs. 70 & 71), whereas all the larvae developed normally in the LD photoperiod by 1 September and in the SD photoperiod by 3 November 1977. In the 1978 cohort the larva (n = 1) collected 1 April and set up at the LD photoperiod developed at the normal rate. On 27 April only half the larvae in the LD photoperiod (n = 10) developed at the normal rate and none of the larvae in the SD photoperiod (n = 4) developed at this rate.

The mean duration for development in the F instar normal development group (Fig. 72) was similar at both photoperiods for a given date during the study. The mean duration for development decreased from 2 August to 3 November, then increased, but decreased again by 3 February.

The mean duration for development in the F instar prolonged development group (Fig. 72) was greater in the SD photoperiod (45 days) on 27 April 1978, than at any other time during the study (25 to 35 days).

F instar 'metamorphosis' During the above experiments with the F instar larvae observations were also made on the time required for the completion of development from early metamorphosis to emergence. No larvae required longer than X_{max} (13 days) to complete development in the laboratory. The rate of development was similar at both photoperiods and varied only slightly during the year with no apparent seasonal trend. Detailed studies concerning possible seasonal changes in the duration of this metamorphosis stage and further analyses of the results were therefore considered unnecessary.

7.3.3.4. Comments - Isaac's Pond The mortality trends and the changes in the mean duration for development in the normal development groups are discussed in a general fashion and are related to the corresponding comments that were made on the results from Lake Sarah - tb (section 7.3.3.2.). The use of the X_{max} value to

Fig. 70. Percentage mortality and percentage of the larvae showing normal development in the F instar of *Xanthocnemis zealandica* from Isaac's Pond, maintained at LD 20°C.

Fig. 71. Percentage mortality and percentage of the larvae showing normal development in the F instar of *Xanthocnemis zealandica* from Isaac's Pond, maintained at SD 20°C.

The number of larvae set up and the number responding (in brackets) in each experiment is indicated above the respective collection date.

Symbols:

circle - normal development

square - mortality

hollow - LD photoperiod

solid - SD photoperiod.

Fig. 72. The mean duration (days) from collection to completion of the F stadium (up to early metamorphosis) of *Xanthocnemis zealandica* larvae from Isaac's Pond (± one standard deviation shown).

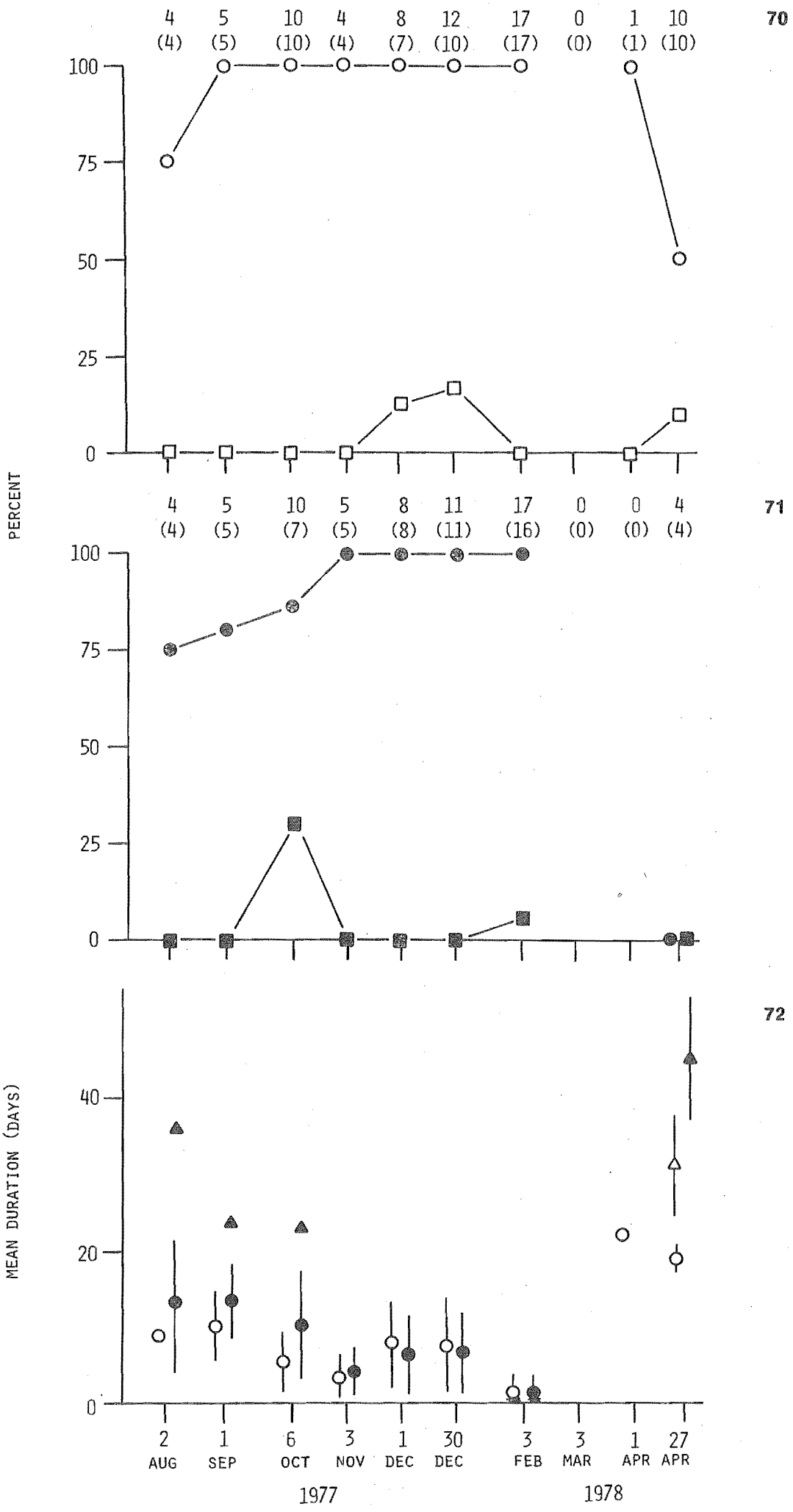
Symbols:

circle - normal development

triangle - prolonged development

hollow - LD 20°C

solid - SD 20°C.


70
4 (4)
5 (5)
10 (10)
4 (4)
8 (7)
12 (10)
17 (17)
0 (0)
1 (1)
10 (10)
100
75
50
25
0
71
4 (4)
5 (5)
10 (7)
5 (5)
8 (8)
11 (11)
17 (16)
0 (0)
0 (0)
4 (4)
PERCENT
72
MEAN DURATION (DAYS)
40
20
0
2 AUG
1 SEP
6 OCT
3 NOV
1 DEC
30 DEC
3 FEB
3 MAR
1 APR
27 APR
1977
1978

distinguish the larvae in the population that developed at the normal or prolonged rates was discussed previously (section 7.3.3.2.) and has not been re-examined here. The development and the response of larvae to photoperiod during the year is discussed instar by instar and is related to the results from Lake Sarah - tb. Because the studies at Isaac's Pond did not encompass a complete year, some of the response patterns obtained were not as evident as those that were observed for larvae from Lake Sarah - tb.

The mortality experienced by the *X. zealandica* larvae from Isaac's Pond did not show the seasonal pattern that was observed at Lake Sarah - tb. At Isaac's Pond the rate of mortality varied considerably during the summer when the larval population developed at the normal rate. Notably, mortality of F-2 and F-1 instar larvae increased during November-December 1977 (Figs. 64, 65, 67 & 68). This was unlike the low mortality observed at Lake Sarah - tb during the period of normal development (*e.g.* 30 July to 8 January 1978, Fig. 61). Mortality usually was relatively high at Isaac's Pond when a high proportion of the population developed at the prolonged rate (see February to early April 1978, Fig. 64 and March to late April 1978, Figs. 67 & 68). Although this was not as consistent a pattern as that observed at Lake Sarah - tb, the trend towards high mortality during the period of prolonged development was similar in the populations at both sites. As mentioned in section 7.3.3.2., this high mortality probably was related to stress experienced by larvae in the prolonged development group, perhaps because they were kept in conditions in the laboratory that were unsuitable to promote a rapid change to the normal development rate.

Initially, a trend that showed seasonally high mortality was considered to be a possible indication of prolonged development in the larval population. For example, high mortality in an experiment possibly indicated that a high proportion of the population was developing at the prolonged rate at the time that the experiment was set up. However, because the rate of mortality at Isaac's Pond varied considerably during the summer when the larval population developed at the normal rate, the use of mortality trends as an indicator of prolonged development in *X. zealandica* was concluded to be unreliable.

The changes in the mean duration for development in the normal development groups were believed to reflect the periods of

larval growth at Isaac's Pond. The studies were started 2 August 1977 when water temperatures were already rising (Fig. 12); therefore, the amount of development that occurred during the winter was unknown. The start of emergence by mid-August 1977 (Table 9) and the larval survey (see June to August, Fig. 16) indicated that development occurred during the winter.

The start of rapid development in the F-2 instar larvae took place between August and September (Fig. 66), probably because of rising water temperature. This indicated that the threshold temperature for development of F-2 instar larvae was higher than or close to the temperatures experienced during at least June and July (approximate mean water temperature 9 to 10°C). The mean duration for development of the F-2 instar larvae showed a marked decrease when the temperature permitted growth during August-September. No period of rapid development was noted in the F to early metamorphosis and F-1 instar larvae (Figs. 72 & 69, respectively), possibly because larvae in these instars continued development at a slow rate during the winter. The information necessary to confirm that development of these instars occurred during the winter was not available because experiments were not set up prior to 2 August 1977. However, these observations suggested that the threshold temperature of F-2 instar larvae was higher than those of the F to early metamorphosis and F-1 instar larvae. This, combined with the comments made in section 7.3.3.2., supported the threshold temperature results (section 7.3.1.) that indicated the highest threshold temperature for the F-2 and lowest threshold temperature for the F-1 instar larvae of the stages tested (see Table 22).

Corbet (1957c) suggested that synchronisation of emergence of *Coenagrion mercuriale* (Charp.) and *Ceriagrion tenellum* (Villers) was achieved by a rising series of lower temperature thresholds (threshold temperature for development) for successive developmental stages in spring. This response was definitely shown to occur in *Lestes eurinus* Say (Lutz 1968b) which supported Corbet's LTT hypothesis. In the present study, the later successive developmental stages of *X. zealandica* do not have a rising series of threshold temperatures; therefore, rising temperatures during the spring would not synchronise emergence.

The slow decrease of the mean duration for development during the period from August-September to November-December (Figs. 66, 69 & 72) was probably related to a progressive reduction in the rate of recruitment into the later instars. Speculatively, the sequence of events that produced this pattern probably was as follows. As temperatures rose development continued and moulting took place. When the recruitment into a later instar was relatively high then the mean duration for development of the larval population in that instar probably increased because of the large influx of developmentally young larvae. However, when the recruitment into a later instar was relatively low then the mean duration for development of the larval population in that instar probably continued to decrease because of the small influx of developmentally young larvae.

An instar frequency distribution that possibly produced the pattern of decreasing mean duration for development that was noted above was, for example, that of cohort 2 for August 1976 (Fig. 15) when the percentage composition of each instar in the population destined to emerge during 1976-1977 was: 21.2% in F; 44.6% in F-1; 20.1% in F-2; and 13.1% in F-3 to F-5. A relatively large proportion of the population was present as F-1 instar larvae; therefore, when they moulted into the F instar the mean duration for development of the F instar larval population would increase. For the remaining instars moulting took place from proportionally smaller to larger populations. The mean duration for development of the F-1, F-2, *etc.* instar larvae would decrease slowly until each instar disappeared from the population.

The pattern of development for the F instar larvae up to early metamorphosis in the normal development group during October to February (Fig. 72) was similar to that discussed previously for the F instar population at Lake Sarah - tb during October to January (Fig. 63). At Isaac's Pond, the increased mean duration and standard deviation for development on 1 December 1977 (Fig. 72) was believed to indicate a substantial recruitment into the F instar, probably during November (see p.147). The marked decrease of the mean duration for development by 3 February 1978 indicated a reduction or a complete cessation of recruitment into the F instar during January, which was about a month later than observed at Lake Sarah - tb (see 8 January, Fig. 63). The late entry of larvae into the F instar at Isaac's

Pond probably resulted in the slightly later end of emergence than at Lake Sarah - tb (Table 9).

The development and response of larvae during the year is discussed now. The environmental factors likely to affect the response of the larvae are considered and the results are related to those from Lake Sarah - tb (section 7.3.3.2.). Implications are suggested, but the final discussion of the significance of these results is left for section 7.3.4..

F-2 instar Prolonged development in the F-2 instar larvae at Isaac's Pond was first evident 3 February 1978 (Fig. 64) at the time of the appearance of this instar in the new cohort. The mean water temperature was relatively stable during January to March 1978 (Fig. 12), being about 17°C; therefore, the induction of prolonged development was probably cued by photoperiod, as was suggested for this instar in the population at Lake Sarah - tb.

At Isaac's Pond, all the larvae tested changed to development at the normal rate by 1 April 1978 (Figs. 64 & 65). Because this occurred before the water temperature started to decrease (Fig. 12), the equinoctial photoperiods probably cued this change.

The proportion of the F-2 instar larval population in the prolonged development group was approximately 50% in both photoperiods on 3 March 1978 (Figs. 64 & 65). This was similar to the proportions noted at Lake Sarah - tb, 20 March 1977 (Figs. 55 & 56). Apparently, there was no differential response to photoperiod at either site by March. Confirmation of a differential sensitivity to photoperiod during January and February, as observed at Lake Sarah - tb (Figs. 55 & 56), was not possible at Isaac's Pond. During this period F-2 instar larvae were scarce in the Isaac's Pond population; therefore, sufficient numbers for experiments could not be obtained.

The intensity of the prolonged development response (approximate mean duration 80 days, Fig. 66) was similar to the response observed at Lake Sarah - tb (Fig. 57) and was similar at both photoperiods, possibly for the reasons suggested earlier (p.150).

These observations showed that:

- a growth restriction occurred in the F-2 instar larvae at Isaac's Pond during February-March which was not indicated in the larval survey (section 4.3.1.); and
- only slight differences, if any, in the prolonged development response occurred between the F-2 instar populations at Isaac's Pond and at Lake Sarah - tb.

F-1 instar Prolonged development in the F-1 instar larvae at Isaac's Pond was first evident 3 March 1978 (Figs. 67 & 68) at the time of the appearance of this instar in the new cohort. As suggested for the larvae in the F-2 instar at both sites and in the F-1 instar at Lake Sarah - tb, the induction of prolonged development was probably cued by photoperiod.

The timing of the change to development at the normal rate was not observed at Isaac's Pond in either photoperiod; however, the change probably occurred between late April and early August from year to year. Approximately half of the larvae developed at the prolonged rate during April 1978, whereas all the larvae developed normally by August 1977 (Figs. 67 & 68). This was similar to the response of larvae from Lake Sarah - tb in the SD photoperiod (Fig. 59) but the change occurred earlier, by late April, in larvae in the LD photoperiod (Fig. 58). The later change to normal development by larvae from Isaac's Pond in the LD photoperiod was believed to be an indication that a combination of autumnal photoperiods and falling temperatures was necessary to promote the completion of prolonged development in F-1 instar larvae. This combination of environmental cues was not clearly shown at Lake Sarah - tb because the temperature decreased rapidly between March and April 1977 (Fig. 13).

The larvae from Isaac's Pond showed a differential response to photoperiod during March and early April; a greater proportion of the larvae developed at the prolonged rate in the SD photoperiod (Fig. 68), than in the LD photoperiod (Fig. 67). This sensitivity to photoperiod indicated that the prolonged development response was facultative.

The intensity of the prolonged development response was dissimilar at the two photoperiods with larvae from Isaac's Pond (Fig. 69) and from Lake Sarah - tb (Fig. 60). However, unlike larvae in the LD photoperiod collected up to late March at Lake Sarah - tb (Fig. 60), the larvae from Isaac's Pond did not show a strong prolonged development response (mean greater than 100 days) in the LD photoperiod on 3 March 1978 (Fig. 69). Unfortunately, because F-1 instar larvae were scarce at Isaac's Pond on 3 March 1978, the sample was small (n = 6) and only one larva showed prolonged development in the LD photoperiod. This individual died after 95 days in the laboratory; therefore, the intensity of the prolonged development response probably was strong at this time and perhaps was similar to

the strong response observed at Lake Sarah - tb.

If a strong prolonged development response occurred in larvae from Isaac's Pond on 3 March 1978 in the LD photoperiod, then a major change in response, probably cued by photoperiod, took place during the period of the autumnal equinox. As at Lake Sarah - tb (Fig. 60), the larvae from Isaac's Pond showed a weak prolonged response in the LD photoperiod after March (Fig. 69). The weak and strong prolonged development responses indicated a minor and a major developmental restriction in the F-1 instar larvae that was common to both study sites.

The above observations showed that:

- a growth restriction occurred in the F-1 instar larvae at Isaac's Pond during March as was previously indicated by the larval survey (section 4.3.1.); and
- only slight differences in the prolonged development response occurred between the F-1 instar populations at Isaac's Pond and at Lake Sarah - tb.

F instar up to early metamorphosis Prolonged development in the F instar at Isaac's Pond was first evident 27 April 1978 (Figs. 70 & 71) shortly after the appearance of this instar in the new cohort. The experiment set up 1 April 1978 consisted of one larva only; because F instar larvae were virtually absent from the Isaac's Pond population at that time. Therefore, the indication that 100% of the larvae (n = 1) developed at the normal rate (Fig. 70) must be treated with reserve. A larger sample is required before further comment can be made about the incidence of prolonged development during early April. The induction of prolonged development on 27 April was probably cued by photoperiod, although a slight decrease in water temperature occurred at Isaac's Pond during April 1978 (Fig. 12) which may have interacted with photoperiod to affect the rate of development.

The pattern of the change to normal development that occurred during 1977 at Isaac's Pond (Figs. 70 & 71) was similar to that observed for the F instar larvae at Lake Sarah - tb (Figs. 61 & 62). The proportion of the population at Isaac's Pond that developed at the normal rate increased slowly from month to month, at a similar rate in both photoperiods. All the larvae developed at the normal rate by September-October. Some factor in addition to exposure to cool conditions during the winter was probably responsible for the change to

normal development. This change occurred at a regular rate, without a distinct transition period and it ended slightly earlier at Isaac's Pond (September-October) than at Lake Sarah - tb (October). Perhaps the final stimulus for normal development comes from rising temperatures during the spring, or from the increasing photoperiods at that time.

The larvae showed a differential response to photoperiod on 27 April 1978; a greater proportion of the larvae developed at the prolonged rate in the SD photoperiod (Fig. 71) than in the LD photoperiod (Fig. 70). This sensitivity to photoperiod indicated that the prolonged development response was facultative.

The intensity of the prolonged development response was dissimilar at the two photoperiods (Fig. 72), as at Lake Sarah - tb (Fig. 63); however, the timing and the intensity of this response apparently differed between the two sites. At Isaac's Pond on 27 April 1978, the larvae showed a strong response in the SD photoperiod (mean duration 45 days), whereas in the LD photoperiod at this time and in the other SD and LD experiments the larvae showed a weak response (mean duration 25 to 35 days). As at Lake Sarah - tb, these differences in the intensity of the prolonged development response in the two photoperiods indicated that the response was facultative.

The strong prolonged development response at Lake Sarah - tb (mean duration 55 days) on 20 March 1977 (Fig 63) occurred earlier and was stronger than at Isaac's Pond. A similar relationship between time of collection and intensity of prolonged development was evident for all the instars examined at both sites. Generally, if the new cohort appeared early during the period from January to April then the prolonged development response was strong (Figs. 57, 60, 63, 66, 69 & 72). Photoperiod probably was the cue responsible for this trend; day length steadily decreased during this period (Fig. 14), whereas water temperature remained relatively constant depending on the site (Figs. 12 & 13).

The strong prolonged development response was noted later in the season (27 April) in the F instar larvae at Isaac's Pond than at Lake Sarah - tb (20 March). The equinoctial photoperiod was previously considered to be the principal cue that terminated the strong response at Lake Sarah - tb; however, the results from Isaac's Pond indicated that the combination of autumnal photoperiods and falling temperatures probably was responsible for the termination of the strong response.

These observations on the F instar larvae showed that:

- a growth restriction occurred in the larvae at Isaac's Pond during April which was not indicated in the larval survey (section 4.3.1.); and
- only slight differences in the prolonged development response occurred between the population at Isaac's Pond and at Lake Sarah - tb.

F instar 'metamorphosis' The comments made earlier (p.153) for the larvae in this stage from Lake Sarah - tb are also applicable to the larvae from Isaac's Pond.

7.3.4. Prolonged Development

The following section (7.3.4.1.) applies to the F-2, F-1 and F (up to early metamorphosis) instar larvae of *X. zealandica* unless otherwise specified. This section is based on the combined observations from Lake Sarah - tb and Isaac's Pond (section 7.3.3.) and is presented as a generalised overview of the prolonged development response of *X. zealandica*.

7.3.4.1. General characteristics Prolonged development occurred during or after January at the time when larvae in the instars tested first appeared in the new cohort. If F or F-1 instar larvae appeared early during this period then a high proportion of the population showed prolonged development at both the LD and SD photoperiods in the laboratory. This indicated that the larvae were insensitive to the fixed photoperiods in the laboratory; therefore, prolonged development was induced by conditions that the larvae experienced in the field at the time of collection. Because the water temperature was relatively constant and high (15-17°C) and food was abundant, the environmental cue considered likely to induce prolonged development was the rate of decrease of the day length in the field.

After the summer solstice (approximately 21 December) the day length begins to decrease and the rate of decrease accelerates until the autumnal equinox (approximately 21 March). The rate of decrease then decelerates until the winter solstice (approximately 21 June) after which the day length begins to increase. The prolonged development response was probably cued by the accelerating rate of decrease experienced during January-March. However, further experiments with larvae using carefully controlled temperatures and naturally occurring photoperiods must be carried out to ascertain

whether the rate of decrease of day length is the environmental cue that induces prolonged development in *X. zealandica*.

Corbet (1955, 1956a) suggested that *A. imperator* larvae were sensitive to a day length increment of about two minutes per day. Below this rate diapause was induced, *i.e.* in decreasing, constant, or natural photoperiods (after the end of May in southern England), whereas above this rate diapause was averted, *i.e.* in natural photoperiods during spring. Induction of prolonged development in *X. zealandica* evidently differs from the above (see p.168), nonetheless it represents the second record of response to changing day length in the Odonata. Perhaps this type of response is related to the length of life cycle as suggested by Corbet (1962,p.95). Both species are semivoltine; therefore, recognition of spring or autumn photoperiodic regimens is required, probably to prevent emergence during the autumn (see section 8.).

In the present study, the F-2 instar larvae showed a differential response to photoperiod during January-February (see Figs. 55 & 56), unlike the F and F-1 instar larvae. Different proportions of the F-2 instar population developed at the prolonged rate in the LD and SD photoperiods on a given date; however, prolonged development did occur at both photoperiods. This indicated that F-2 instar larvae were sensitive to fixed photoperiods and to the rate of decrease of day length. Therefore, both of these factors were believed to cue prolonged development of larvae in this instar.

Although prolonged development was induced by conditions experienced in the field, the intensity of the subsequent response often was affected by the fixed photoperiods in the laboratory. For example, all the F instar larvae collected on 20 March 1977 developed at the prolonged rate in both photoperiods (Figs. 61 & 62); however, a strong response was shown in the SD photoperiod only (Fig. 63). The intensity of the prolonged development response exhibited at the two fixed photoperiods changed during the period from January to March-April. This was believed to reflect changes in the sensitivity of the larvae to photoperiod, caused by conditions in the field. F instar larvae showed a strong prolonged response to the SD photoperiod only at the time of the autumnal equinox; F-1 instar larvae showed a strong prolonged response to both periods during January and to the LD photoperiod up to the time of the equinox; and F-2 instar larvae showed the same response to both photoperiods up to the time of the equinox. The strength of the response that larvae showed to absolute day length in the field was not determined in these

studies. It was assumed that the day lengths experienced during January to early March would elicit a LD photoperiod 'type' response and those that occurred during late March and later would perhaps elicit a SD photoperiod 'type' response. Therefore, F instar larvae would show the strong prolonged response during late March and April; F-1 instar larvae would show a strong prolonged response up to some date near the equinox; and F-2 instar larvae would show the same response throughout.

The termination of the strong prolonged development response usually occurred near the time of the autumnal equinox. Only F instar larvae from Isaac's Pond, collected on 27 April 1978 (Fig. 72) showed a strong response after the equinox.

The primary environmental cue for the termination of the strong prolonged development response was not temperature, because temperature was still relatively high at Isaac's Pond during the autumnal equinox when termination occurred in the F-2 and F-1 instar larvae; nor was the cause the absolute day length experienced in the field, because of the nature of the responses observed for larvae at the fixed photoperiods in the laboratory. For example, the F-2 instar larvae developed at the prolonged rate in the LD and SD photoperiod up to the autumnal equinox, whereas afterwards they developed normally at both photoperiods (Fig. 57 & 66). Similarly, the F instar larvae at Lake Sarah - tb developed at the strong prolonged rate in the SD photoperiod at the time of the equinox, whereas afterwards they developed normally or showed a weak prolonged development response (Fig. 63) at this photoperiod.

As mentioned earlier in this section, the accelerating rate of decrease of day length up to the autumnal equinox was believed to cue the onset of prolonged development. Perhaps the decelerating rate of decrease of day length after the autumnal equinox cued the end of prolonged development, or at least the end of the strong response, in the F-2 and F-1 instar larvae respectively. Larvae in the F instar probably required a combination of the decreasing rate of change of day length and cool conditions to cue the end of prolonged development as indicated by results showing the continuation of this response until April at Isaac's Pond (see p.167). Therefore, strongly prolonged development occurred up to the autumnal equinox in the F-1 or earlier instar larvae and up to the onset of cold conditions in the F instar larvae. Additional experiments, similar in nature to those described

earlier to confirm that photoperiod cued the initiation of prolonged development, are required to test the hypothesis that the decelerating rate of decrease of day length caused the termination of prolonged development.

The period for weak prolonged development and for a progressively decreasing proportion of the population that developed at the prolonged rate occurred from April to mid-winter (July) in the F-1 instar larvae (Figs. 58 & 59) and from April to approximately October in the F instar larvae (Figs. 61, 62, 70 & 71). The termination of the weak prolonged development response in the F-1 instar larvae probably was caused by exposure to cold. The pattern of the progressively decreasing proportion of the population that developed at the prolonged rate indicated that some larvae, because of age and/or past experience (dependent on conditions experienced in the micronabitats at the study sites), completed the change to normal development faster than others. The larvae probably needed a definite period of exposure to temperatures (perhaps within a specific range) to fulfil certain physiological requirements before the weak prolonged development response was terminated. A similar response to cold probably occurred in the F instar larvae, because the pattern of change to normal development was similar. However, the final stimulus that terminated the weak prolonged development response probably was rising temperature because prolonged development ended earlier at Isaac's Pond (where temperatures started rising earlier) than at Lake Sarah - tb.

The complex nature of the termination of the weak prolonged development response indicates that the weak response is an integral component of prolonged development. The strong response requires the correct photoperiod for termination, whereas the weak response requires a definite period of exposure to cool conditions for termination. Therefore, larvae in the field experience a strong developmental restriction up to the onset of cool conditions and then a continuing weak restriction occasionally up to the onset of rising temperatures. These facts show that the emergence of the individual from Isaac's Pond between 27 June and 5 July 1976 (p. 74) probably represents a rare occurrence.

7.3.4.2. Prolonged development as a form of diapause A definition of diapause was presented early in section 1. for use in this work. Briefly this definition stated that diapause is a physiological condition that is anticipatory of conditions that are

unsuitable for growth. It is usually induced by photoperiod in the Odonata and is not terminated by temperatures becoming permissive for growth but requires a certain time to elapse and certain physiological requirements to be fulfilled (see Ingram & Jenner 1976a; Corbet 1978). For additional descriptions and discussions of diapause see: Andrewartha (1952); Lees (1955, 1956, 1968); de Wilde (1962, 1970); Danilevskii (1965); Beck (1968); Bradshaw (1969, 1970, 1973); Danilevskii *et al.* (1970); Müller (1970); Mansingh (1971); Bradshaw & Lounibos (1972); Tauber & Tauber (1973, 1976); Thiele (1973); Saunders (1976); and see Dingle (1978).

Insects undergoing diapause usually are identified on the basis of the negative criteria of suppressed developmental and metabolic rates (Beck 1968). This requires that the 'normal' non-diapause developmental or metabolic rates are known before the diapause rates can be recognised. Beck (1968) stipulated that rates were *suppressed* rather than *arrested* (Andrewartha 1952; Lees 1955, 1956) because he recognised the necessity to allow for different degrees or intensities of diapause. The use of the term 'suppressed' also accounted for any growth and development processes that occurred during diapause (see diapause development, Andrewartha 1952) and furthermore applied meaningfully to instances where developmental rates were measurable, although slow, and the insect was in a state of diapause.

The prolonged development response of *X. zealandica* is now examined with respect to the above criteria. The physiological condition of the animals that developed at the prolonged rate was not determined in these studies. The response was anticipatory of conditions unsuitable for growth, because prolonged development occurred at a time when temperatures were suitable for growth and food was abundant. The response was probably induced by the accelerating rate of decrease of day length experienced in the field between the summer solstice and autumnal equinox. The intensity of prolonged development differed in the various instars. The F-2 instar larvae showed only one intensity of response, whereas the F-1 and F instar larvae showed a strong or weak response. Warm conditions in the field (15-17°C) or in the laboratory (20°C) failed to terminate prolonged development. The decelerating rate of decrease of day length experienced in the field after the autumnal equinox probably terminated the response in the F-2 instar larvae and the strong response in the F-1 instar larvae, whereas a combination of this day length decrease and falling temperatures terminated the strong response in the F instar larvae.

The weak response in the F-1 and F instar larvae was terminated after a period of exposure to cool conditions that perhaps were needed to fulfil certain physiological requirements.

The time required for the completion of development of larvae in the laboratory was compared with a value (X_{max}) that was considered to be the upper limit for normal development at 20°C, calculated at a probability level of 0.05. Definite suppressed developmental rates, as well as different intensities of suppression were obtained during the year (*i.e.*, the strong or weak prolonged development response in the F-1 and F instar larvae).

The above factors fit the criteria describing diapause; therefore, prolonged development in *X. zealandica* is considered to be a form of diapause. The period of occurrence of diapause (summer-autumn) and the specific stimulus that is required to terminate it (probably primarily a decelerating rate of decrease of day length) indicate that this is 'oligopause' (Müller 1970; Thiele 1973) of an 'aestival type' (Tauber & Tauber 1976). The implication of this is that the suppressed development of late instar larvae during the period from January to March prevents metamorphosis and therefore also emergence during the autumn at a time when the success of subsequent maturation and reproduction is doubtful. It is unnecessary for the larvae of *X. zealandica* to overwinter in a state of diapause.

Recently a cautious approach has been taken with regard to the use of the term 'diapause' in reference to the Odonata. Lutz (1974a) concluded that the presence of a true diapause stage in *T. cynosura* could not be ascertained, although he noted that "larval development was significantly suppressed in animals collected at certain times of the year.". Norling (1976) similarly avoided use of the term 'diapause' in his study of the seasonal regulation of *Leucorrhinia dubia* (Vand. Lind.). However, Ingram & Jenner (1976a) considered the suppressed developmental rates of *E. aspersum* and *E. hageni*, that were induced by day length, to be a manifestation of diapause. I consider the use of the term 'diapause' to be justified in reference to prolonged development in *X. zealandica* and I strongly recommend the use of this term in cases when a seasonal cycle of suppressed development, induced by photoperiod, is evident.

7.4. *AUSTROLESTES COLENSONIS*

See section 7.2. for methods and analyses used here.

7.4.1. Normal Rate of Development

7.4.1.1. Results The number of larvae obtained for distribution among the seven temperature conditions, their percentage mortality and when possible the degree days, threshold temperature and maximum duration for normal development at 20°C (X_{max}) of larvae in the instars F-3, F-2, F-1, and F up to early metamorphosis, and from early metamorphosis to emergence, are presented in Table 23. The linear regression line for the relationship between rate of development and temperature and the equation for this line is presented for the latter three stages mentioned above in Figs. 73 to 75.

TABLE 23. Normal rate of development in the LD photoperiod of *Austrolestes colensonis* larvae.

Instar or Stage	Number set up	Mortality (%)	Degree Days Required to Complete Instar or Stage	Threshold Temperature (°C)	X_{max} (days) at 20°C (P = 0.05)
F-3	13	69	-	-	-
F-2	18	83	-	-	-
F-1	50	68	149.3	9.6	29
F to early metamorphosis	50	58	158.7	8.0	24
F from early metamorphosis to emergence	21	33	94.3	8.2	14

7.3.1.2. Comments The mortality of the stages tested (Table 23) was higher than that observed for *X. zealandica* (Table 22); however, a similar trend was obtained. Mortality was highest in the early instar (F-3 and F-2) larvae and progressively decreased to become lowest in the F instar larvae during metamorphosis (Table 23).

Fig. 73. Relationship between temperature and rate of development of *Austrolestes colensonis* F-1 instar larvae. The equation and calculated linear regression line with 95% confidence limits are shown.

Fig. 74. Relationship between temperature and rate of development of *Austrolestes colensonis* F instar larvae up to early metamorphosis. The equation and calculated linear regression line with 95% confidence limits are shown.

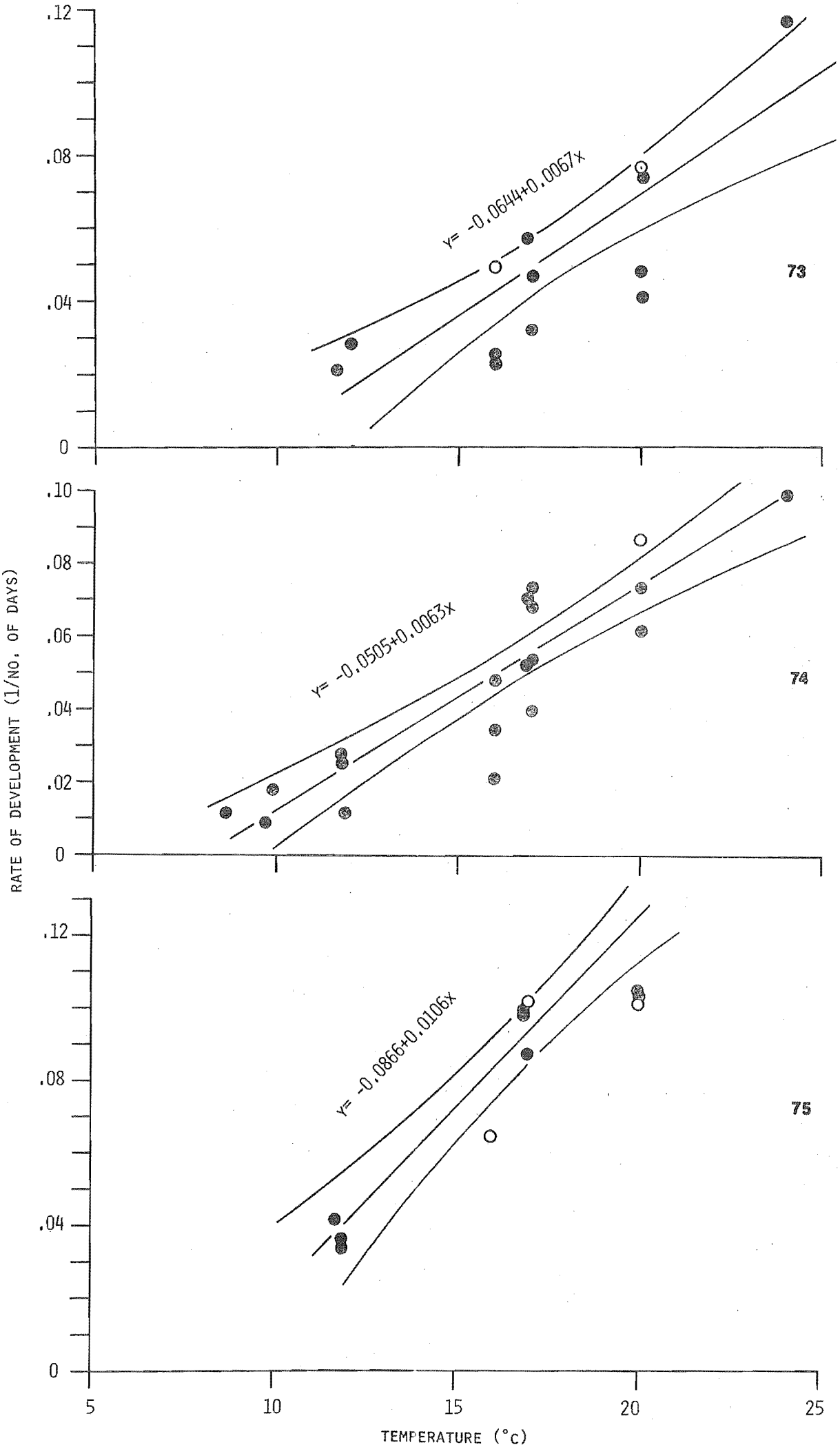
Fig. 75. Relationship between temperature and rate of development of metamorphosis in *Austrolestes colensonis*. The equation and calculated linear regression line with 95% confidence limits are shown.

Symbols:

solid circles - one observation

hollow circles - two observations

hollow circles with central dot - three observations.


.12
.08
.04
0
Y= -0.0644+0.0067x
73
.10
.08
.06
.04
.02
0
Y= -0.0505+0.0063x
74
.12
.08
.04
0
Y= -0.0866+0.0106x
75
5
10
15
20
25
TEMPERATURE (°c)
RATE OF DEVELOPMENT (1/NO. OF DAYS)

Apparently the early instar larvae were not as 'hardy' as the late instar larvae and overall *A. colensonis* was not as easily maintained in the laboratory as *X. zealandica*.

Difficulties in obtaining F-4 and F-3 instar larvae of *A. colensonis* and the high mortality in the subsequent F-3 and F-2 instar larvae resulted in small sample sizes. Therefore, regression analyses were not attempted and a reliable estimate of the duration for normal development at 20°C (X_{max}) could not be calculated.

The linear relationships between the rate of development of the various stages tested and temperature (Figs. 73 to 75) were all highly significant ($P<0.001$).

The threshold temperature for development of F-1 instar larvae was calculated to be 9.6°C; however, no larvae set up at approximately 10°C (n = 6) completed development and only two out of seven completed development at 12°C. This may indicate that the calculated threshold temperature is too low; the true threshold probably lies between 10 and 12°C. The X_{max} value at 20°C (29 days) is based on a sample size of six and is believed to be a reasonable estimate of the maximum duration for normal development.

The threshold temperature for development of F instar larvae up to early metamorphosis was calculated to be 8.0°C which was probably a reliable estimate. Only one larva out of seven completed development at 8.6°C which indicated that this temperature was close to the true threshold. The X_{max} value at 20°C (24 days) (n = 4) was similar to that calculated for the corresponding stage in *X. zealandica* and was believed to be a reasonable estimate of the maximum duration for normal development.

Both the F-1 (n = 8) and F (n = 8) instar larvae experienced high mortality (87 . 5%) at 24°C in the above experiments. This indicated either that 24°C was close to the upper lethal temperature for these later instar larvae, or that the larvae were intolerant of stress (maintenance in the laboratory), combined with a relatively high temperature (24°C). Hodgkin & Watson (1958) found that *Austrolestes* spp. in Australia completed development in temporary ponds that experienced temperatures up to approximately 21 to 27°C during the early summer. Similarly, Barclay (1966) noted that *A. colensonis* near Auckland, New Zealand, emerged from a temporary pond that experienced temperatures up to 27 to 29°C (recorded from approximately 2.5cm below the surface) during November-December.

This tolerance of high temperatures in the field refutes the hypothesis that 24°C was close to the upper lethal temperature for *A. colensonis*. Therefore, the combination of stress plus 24°C probably caused the high mortality.

The threshold temperature for development of F instar larvae from early metamorphosis to emergence was calculated to be 8.2°C; however, during these experiments only three larvae completed development to early metamorphosis at temperatures below approximately 12°C (Fig. 74) (n = 14) and no larva completed metamorphosis at these temperatures (Fig. 75). The threshold temperature for metamorphosis and emergence probably lies closer to 12°C than to 8°C. The X_{max} value at 20°C (14 days) (n = 4) was believed to be a reasonable estimate regardless of the small sample size and was similar to the corresponding stage in *X. zealandica*.

The threshold temperatures for development of the F-1 and F instar larval stages lie between 8 and 12°C. This indicates that growth would continue during the winter at Isaac's Pond, whereas at Lake Sarah - tb growth would not take place until the following spring. Although no larval study was carried out at Isaac's Pond, the threshold temperatures indicate the possible growth pattern at this site, and they support the results obtained for larval growth in the field during the winter at Lake Sarah - tb (section 4.4.1.).

7.4.2. Prey Consumption

7.4.2.1. Results Observations were made on four larvae (number of observations = 35) in the LD, and four larvae (number of observations = 35) in the SD photoperiod conditions. The mean and standard deviation of the number of *O. fuscus* larvae eaten per individual per day was 4.46 ± 2.70 in the LD photoperiod conditions and 3.77 ± 1.96 in the SD photoperiod conditions.

7.4.2.2. Comments The critical U-value was 720 and the calculated U-value was 779.4, which indicated that there was no siginficant difference ($P>0.05$) between the feeding rates of larvae in the two samples. Prey consumption apparently was not related to the day lengths tested; therefore, this relationship could be eliminated as a possible factor affecting the developmental rate of the larvae.

7.4.3. Seasonal Response to Photoperiod

The results from the field work at Lake Sarah - tb indicated that a possible growth restriction occurred in the F-2 or earlier instar larvae of *A. colensonis* (section 4.4.1.2.) which prevented moulting into the F-1 instar and ended emergence by March (section 5.4.1.2.). A laboratory study, similar to that carried out on *X. zealandica* (section 7.3.3.), was designed to examine the nature of this growth restriction in the F-2 instar larvae.

Initially larvae earlier than the F-2 instar were to be examined, but because of high mortality this study was confined mainly to F-2 instar larvae. The X_{max} value for the F-2 instar was not obtained; therefore, the presentation of the results in this section had to be altered from that used earlier (section 7.3.3.). Because normal or prolonged rates of development could not be distinguished, the mean duration for the completion of development (± one standard deviation) for all the larvae in each photoperiod on a given date was calculated and graphed. These results were then examined for possible indications of a growth restriction, especially during January to April.

7.4.3.1. Results The mean duration for development of the F-2 instar larvae is presented in Fig. 76. The numbers along the top of the graph indicate:

- larvae in the LD photoperiod - upper series;
- larvae in the SD photoperiod - lower series;
- larvae that were set up - unbracketed number; and
- larvae that completed development - bracketed number.

The F-2 instar larvae were scarce at Lake Sarah - tb from December 1977 to February 1978 and during February 1977 (Fig. 76); however, the number of larvae started to increase by March 1977 and adequate numbers for experiments were obtained from June to October 1977. Larvae seldom required more than 25 days to complete development and the response of the larvae at either photoperiod was similar.

Three out of the seven larvae that responded in each of the LD and SD photoperiods on 20 March and 27 April 1977 went through supplementary moults to reach the F-1 instar. By 1 June 1977 two out of three larvae made supplementary moults in the LD photoperiod only. This phenomenon was not observed again in the subsequent experiments.

Fig. 76. The mean duration (days) from collection to completion of the F-2 stadium of *Austrolestes colensonis* larvae from Lake Sarah - tb (± one standard deviation shown).

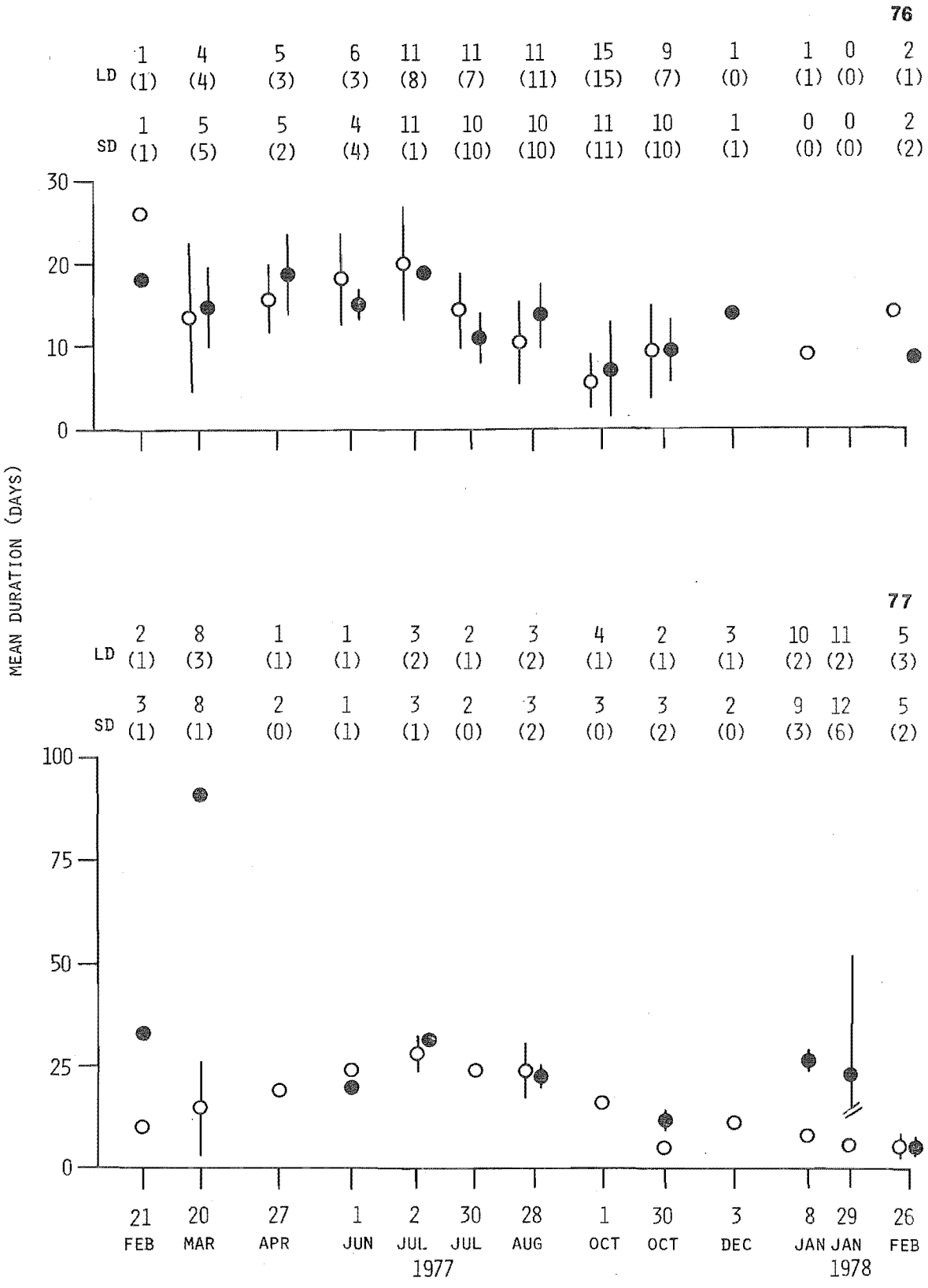
Fig. 77. The mean duration (days) from collection to completion of the F-1 stadium of *Procordulia smithii* larvae from Lake Sarah - tb (± one standard deviation shown).

The number of larvae set up and the number responding (in brackets) in each experiment (LD photoperiod - upper series; SD photoperiod - lower series) is indicated above the respective collection date.

Symbols:

hollow - LD photoperiod

solid - SD photoperiod.


76
LD 1 (1) 4 (4) 5 (3) 6 (3) 11 (8) 11 (7) 11 (11) 15 (15) 9 (7) 1 (0) 1 (1) 0 (0) 2 (1)
SD 1 (1) 5 (5) 5 (2) 4 (4) 11 (1) 10 (10) 10 (10) 11 (11) 10 (10) 1 (1) 0 (0) 0 (0) 2 (2)
77
LD 2 (1) 8 (3) 1 (1) 1 (1) 3 (2) 2 (1) 3 (2) 4 (1) 2 (1) 3 (1) 10 (2) 11 (2) 5 (3)
SD 3 (1) 8 (1) 2 (0) 1 (1) 3 (1) 2 (0) 3 (2) 3 (0) 3 (2) 2 (0) 9 (3) 12 (6) 5 (2)
MEAN DURATION (DAYS)
30
20
10
0
100
75
50
25
0
21 FEB
20 MAR
27 APR
1 JUN
2 JUL
30 JUL
28 AUG
1 OCT
30 OCT
3 DEC
8 JAN
29 JAN
26 FEB
1977
1978

7.4.3.2. Comments Almost no F-2 instar larvae were present in the population during December 1977 to February 1978 at Lake Sarah - tb which indicated that most of the larvae in the emerging cohort completed development into the F-1 instar by early December. Recruitment into the F-1 instar occurred rapidly after the onset of warm weather; the end of recruitment was not related to a growth restriction in the F-2 instar larvae. This latter instar was already absent from the population at the time of the suspected growth restriction.

When the F-2 instar appeared in the population (approximately March) the larvae completed development relatively quickly and responded similarly to either photoperiod in the laboratory. No indication of the prolonged rate of development that was observed in the later instars of *X. zealandica* (section 7.3.3.), was noted in *A. colensonis*. However, the F-2 instar larvae made supplementary moults during March, April and early June which delayed entry into the later instars. Larvae moulted into a stage intermediate between the F-2 and F-1 instars which prolonged development by the amount of time required to complete the development of the added stage.

Supplementary moulting, which was also mentioned briefly in section 2., was considered by Ingram & Jenner (1976a) to be related to prolonged development. Supplementary (extra) moults in *E. hageni* and *E. aspersum* occurred in response to an 11L:13D photoperiod and 21°C conditions. They concluded that the induction of supplementary moults by short day lengths under conditions otherwise favourable for development may be critical in preventing emergence during the late autumn.

Supplementary moulting in *A. colensonis* probably caused the observed synchronisation of the instars within the population. This form of prolonged development possibly occurred in the F-3 or earlier instars as well as in the F-2 instar larvae. An F-3 instar larva that was collected on 8 January 1978 and set up in the LD photoperiod survived and made one supplementary moult before entering the F-2 instar. If a limited number of later instar larvae were affected then extra moulting would slow the development of the most advanced larvae, whereas the less advanced larvae would accumulate in the intermediate stages of the earlier instars. thereby decreasing the range of the instars within the population.

Because of limited results, no attempt was made to identify the principal factors regulating the supplementary moult growth restriction in *A. colensonis*. Most of the comments made about growth restrictions within the larval population (section 4.4.) and their possible effects on emergence (section 5.4.) must remain speculative. A growth restriction apparently does occur and takes the form of supplementary moulting which affects at least the F-2 instar and probably earlier instar larvae.

7.5. *PROCORDULIA SMITHII*

See section 7.2. for methods and analyses used here.

7.5.1. Normal Rate of Development

Only a limited laboratory study was carried out using *P. smithii* larvae. Because of difficulties experienced in obtaining sufficient numbers of larvae, no normal rate of development studies were attempted. No X_{max} value was calculated; therefore, no distinction between normal and prolonged rates of development was possible.

7.5.2. Prey Consumption

7.5.2.1. Results Observations were made on three larvae (number of observations = 29) in the LD, and three larvae (number of observations = 29) in the SD photoperiod conditions. The mean and standard deviation of the number of *O. fuscus* larvae eaten per individual per day was 4.38 ± 3.28 in the LD and 4.52 ± 2.73 in the SD photoperiod conditions.

7.5.2.2. Comments The critical U-value was 464.5 and the calculated U-value was 546.5, which indicated that there was no significant difference ($P>0.05$) between the feeding rates of the larvae in the two samples. Prey consumption apparently was not related to the day lengths tested; therefore, this relationship could be eliminated as a possible factor affecting the developmental rate of the larvae.

7.5.3. Seasonal Response to Photoperiod

The results from the field work at Lake Sarah - tb indicated a possible growth restriction in the F-1 instar larvae of *P. smithii*

(section 4.5.1.2.) which prevented moulting into the F instar from December to February. A laboratory study, similar to that carried out on the F-2 instar larvae of *A. colensonis* (section 7.4.3.), was designed specifically to examine the seasonal response to photoperiod made by *P. smithii* F-1 instar larvae at Lake Sarah - tb. However, a combination of scarcity of F-1 instar larvae in the field and high mortality in the laboratory resulted in small sample size (occasionally n = 1). Because of this, these results must be treated with extreme reserve. They are examined only for indications of a possible growth restriction.

7.5.3.1. Results Most larvae completed development in less than 30 days (Fig. 77). An extreme response (*i.e.*, greater than 35 days) was observed only in the SD photoperiod. One larva collected on 20 March 1977 required 91 days and one larva collected on 29 January 1978 required 81 days to complete development.

7.5.3.2. Comments The above limited results for F-1 instar larvae possibly indicated a differential response to photoperiod and a growth restriction during January to March. This tentatively supported the inferences made during the field work.

The emergence patterns of *A. colensonis* and *P. smithii* were similar; however, the means of attaining these patterns apparently were dissimilar unlike the suggestion that was made earlier (section 5.5.2.2.). Larvae of *A. colensonis* undergo supplementary moulting, whereas larvae of *P. smithii* probably show prolonged development. Therefore, the similarity in the emergence patterns of these two species was not an indication of a similarity in the response of larvae to environmental factors. Further comment about the nature of the growth restriction in *P. smithii* larvae and the effect that it has on emergence is unwarranted because of insufficient information.

8. DISCUSSION

The principal aim of this thesis was to determine the seasonality, primarily of *X. zealandica* and to a lesser degree of the remaining three species, of the odonates studied. The approach taken was to follow the larval growth and the seasonal pattern of emergence under natural conditions to provide an accurate account of seasonality in the field. These results indicated growth restrictions in various life-history stages; therefore, a laboratory study on eggs and larvae was carried out to examine the nature of these responses. The results from the laboratory study confirmed, supported, or refuted the inferences about growth restrictions that were made from the field studies. Life histories, obtained from the synthesis of results from the field and laboratory studies are presented and their interpretations discussed in the following section.

X. zealandica mainly has a two-year life cycle at Isaac's Pond and a three-year life cycle at Lake Sarah - tb. At the latter site *A. colensonis* mainly has a two-year life cycle and *P. smithii* mainly has a four-year life cycle.

Emergence of *X. zealandica* and *A. colensonis* starts earlier during the year at Isaac's Pond than at Lake Sarah, but ends by approximately the same date at all three sites. The seasonal emergence pattern of *X. zealandica* is trimodal at Isaac's Pond, but bimodal at the Lake Sarah sites and has no pronounced peak of emergence within the emergence period. The emergence pattern of *A. colensonis* is bimodal at all three sites and has a peak of emergence at the end of the emergence period. The emergence pattern of *P. smithii* is bimodal and similar to that of *A. colensonis* at Lake Sarah. *P. grayi* has a peak of emergence at the start of a relatively short emergence period.

Embryonic development is direct in *X. zealandica* and *P. grayi* and usually is direct in *A. colensonis*, although some delayed hatching occurs in the latter species. Embryonic development of *P. smithii* is direct above approximately 19-20°C, but greatly prolonged below this temperature. Hatching of *X. zealandica* and *P. grayi* eggs probably occurs only the summer eggs are laid. At Lake Sarah - tb some eggs of *A. colensonis* hatch the summer they are laid and the eggs that survive the winter hatch synchronously the following spring. Most eggs of *P. smithii* overwinter and hatch the following spring.

Development ceases in the later instar larvae of *X. zealandica* at temperatures below approximately 7 to 9°C. The threshold temperature of development is approximately 8 to 12°C in the later instar larvae of *A. colensonis*.

Diapause (possibly cued by the rate of change of day length and temperature) occurs in *X. zealandica* F-2 to F instar larvae during the summer. Also during the summer, supplementary moulting occurs in the F-2 instar larvae of *A. colensonis* and prolonged development (possibly diapause) occurs in the F-1 instar larvae of *P. smithii*. The instars mentioned above were the only stages tested.

A secondary aim of this thesis was to examine the effects that altitudinal differences, expressed as climatic differences, had on the pattern of seasonality of *X. zealandica*. The establishment of accurate accounts of the seasonality of *X. zealandica* at Isaac's Pond (30m above mean sea level) and at Lake Sarah - tb (579m above mean sea level) made this objective possible. Isaac's Pond, because of the local climate and especially because of the artesian water source, experienced long, cool summers and short, warm winters. Lake Sarah - tb, because of the local climate which was influenced by almost continuous winds, altitude and an inland location, experienced shorter summers, that possibly were warmer, and longer, cooler winters than at Isaac's Pond.

There were three main differences in the patterns of seasonality observed between the two study areas.

X. zealandica completed its life cycle in two years at Isaac's Pond, whereas it required three years to complete its life cycle at Lake Sarah - tb.

Seasonal emergence of *X. zealandica* started earlier at Isaac's Pond than at Lake Sarah.

The seasonal pattern of emergence of *X. zealandica* was trimodal at Isaac's Pond, but it was bimodal at Lake Sarah.

Variations in the duration of the life cycles of several aquatic insects have been recorded prior to this study. Three examples have been selected to illustrate these variations.

Perhaps one of the more dramatic examples was the situation that Macan (1964, 1974) described for a population of *P. nymphula* (Coenagrionidae) in Hodson's Tarn. This species had a one- or two-year life cycle when the larval density was low and a three-year life cycle when the larval density was high. A similar pattern of

voltinism was noted in the weed beds in the pond, *i.e.* a two-year life cycle occurred if larvae were found in *Littorella* and a three-year life cycle occurred if larvae were found in *Carex*. Macan concluded that the availability of food regulated the rate at which the population developed.

A second example of variations in the voltinism of a species within the same habitat has been found in the mayfly *Ephemera danica* Müller. Svensson (1977) found that this species took two or three years to complete development in a stream in southern Sweden. He suggested that differential growth rates between cohorts were cued by environmental factors and caused the voltinism observed.

In a third example, Brittain (1978) found that the stonefly *Nemurella pictetii* Klapálek varied in voltinism in habitats at different altitudes. This species had a one-year life cycle in lowland habitats and a two-year life cycle in a mountain habitat. Brittain speculated that the likely causes of the change to a semivoltine life cycle in a mountain habitat were the low temperatures and inferior quality of the food available.

Of the above examples, the third is considered to be similar to the situation observed for *X. zealandica* in this study. Availability or quality of food may have played a role in causing the differences in voltinism observed; however, food appeared to be readily available at all times (although this was not examined specifically) at both Isaac's Pond and Lake Sarah - tb. Growth rates, cued by environmental factors were demonstrated to be similar in the later instar larvae from the two populations (section 7.3.3.). The photoperiod regimen, which at least in part regulated growth rates, was similar at the two sites; therefore, the responses were expected to be similar. However, the temperature regimens experienced at Isaac's Pond and Lake Sarah - tb differed markedly and probably caused the difference in voltinism observed. At Isaac's Pond larvae continued growth and development at a slow rate during the winter and started rapid growth earlier during the spring than at Lake Sarah - tb. Because of this longer, almost continuous, growth season at Isaac's Pond the larvae completed development in two years instead of the three observed at Lake Sarah - tb.

The earlier start of seasonal emergence at Isaac's Pond also was believed to be related to the warmer conditions experienced there, than at Lake Sarah - tb. Larvae entered the F instar during March or

April at both sites but, because of diapause, did not emerge. After the completion of diapause, the larvae continued development, completed metamorphosis and because of the relatively warm temperature regimen experienced during the winter at Isaac's Pond started to emerge during August. At Lake Sarah - tb, little (if any) development took place during the winter; metamorphosis occurred only when temperatures rose during the spring and emergence started during October, considerably later than at Isaac's Pond.

During a study that was carried out in a mountain stream over altitudes ranging from approximately 1500 to 2600m, Nebeker (1971) correlated temperature, as influenced by altitude, with significant changes in the emergence patterns of several species of winter stoneflies. The emergence of some species was delayed four to six months by the colder water at higher elevations. In the present study, Isaac's Pond and Lake Sarah differed in altitude by only 550m. Temperature, as influenced by altitude, probably caused some of the up to three months difference in the start of emergence of *X. zealandica* that was observed at the study sites. However, local effects, especially the artesian water source at Isaac's Pond and the inland location of Lake Sarah, away from the moderating influence of the ocean (see section 3.4.), probably caused most of this difference in the time of the start of emergence.

Temperature differences between Isaac's Pond and Lake Sarah were also believed to be related to the trimodal and bimodal seasonal emergence patterns observed in *X. zealandica*. The long growth season at Isaac's Pond possibly caused a two-year life cycle and a wide range of instars (F to F-5) in the emerging cohort at the start of emergence. This range of instars, combined with the effects of diapause on the population and the relatively warm temperature regimen experienced during the winter may have produced the three modes of emergence (see p.76). The irregularity of the size of the modes from year to year at Isaac's Pond was probably related to the variable temperature regimen experienced each winter (see p.76).

The shorter growth season at Lake Sarah - tb possibly caused a three-year life cycle and a narrower range of instars (F to F-3) in the emerging cohort at the start of emergence. This narrower range of instars, combined with a summer diapause followed by a relatively cold winter probably produced two modes of emergence (see p.77). The regularity of the size of the modes from year to year at Lake Sarah

possibly was related to the termination of summer diapause and the almost immediate onset of cold conditions that prevented growth during the winter (see p.77).

The above discussion suggested that differences in temperature regimens were related to the differences noted in the patterns of seasonality of *X. zealandica* between Isaac's Pond and Lake Sarah. However, the differences in the temperature regimens were not solely attributable to altitude differences. As mentioned earlier local effects at Isaac's Pond and at Lake Sarah probably contributed more to the temperature differences than an altitudinal difference of 550m. This illustrates the necessity for careful monitoring of the environment during an ecological study of this nature. The possibility of substantial variations in the pattern of seasonality of a species, for reasons other than altitudinal or latitudinal differences was clearly indicated.

Two aspects of the life histories incidental to the main theme that I consider to be particularly noteworthy are the polymodal emergence patterns of the various species and the two-year life cycle of *A. colensonis* at Lake Sarah - tb.

Polymodality of emergence has been noted previously in the odonates, and recently Waldbauer (1978) noted that the reported cases probably were caused by the emergence of individuals that belong to different year classes. For example, Corbet (1957b) found that *A. imperator* normally required two years to complete development at the study site; however, a few individuals completed development in one year. At the start of the final growth period the univoltine larvae were comparatively less advanced in development than the semivoltine larvae and, therefore, they emerged slightly later during the emergence period. This later emergence produced a small second mode of emergence in the seasonal pattern of emergence.

A slightly different situation from the above that also produced a small second mode of emergence was found in a population of *E. aspersum* (Ingram & Jenner 1976b). In this case the second mode was caused by a small bivoltine element in an otherwise univoltine population.

Both of the above examples support the suggestion made by Waldbauer (1978). However, the modality of emergence of *X. zealandica*, *A. colensonis* and *P. smithii* in this study was believed to be related to the instar composition of the emerging cohort. It was not caused

by the emergence of individuals in different year classes. The slow growth of the larvae at the relatively cool temperature regimens experienced at the study sites (*e.g.*, the maximum temperature recorded was 23°C) and the wide range of instars in the emerging cohort at the start of emergence probably caused the extremely long emergence periods observed (*e.g.*, *X. zealandica* emerged during approximately a 220-day period at Isaac's Pond) and gave rise to a modality of emergence that corresponded to instar groups (see pp. 75-77, 88, 96).

The significance of the two-year life cycle of *A. colensonis* at Lake Sarah - tb is now considered. Previous work has shown the life cycles of the lestids to be consistently univoltine, *e.g. Lestes sponsa* (Hansemann) (Corbet 1956c); *Lestes rectangularis* Say (Gower & Kormondy 1963); *Lestes eurinus* Say (Lutz 1968a); *Lestes congener* Hagen (Sawchyn & Gillott 1974a); *Lestes unguiculatus* Hagen, *Lestes disjunctus disjunctus* Walk. and *Lestes dryas* Kirby (Sawchyn & Gillott 1974b); and *Lestes vigilax* Hagen, *Lestes disjunctus australis* Walk. and *Archilestes grandis* (Rambur) (Ingram 1976b). The above species were found in temperate latitudes. Usually rapid growth started during the spring and continued up to emergence . Some species that were adapted to life in a temporary habitat (*e.g.*, *L. dryas*) completed the larval stage in less than two months and emerged before the larval habitat dried out and other species in permanent ponds (*e.g.*, *L. unguiculatus* and *L. disjunctus disjunctus* required about 60 days to complete development (Sawchyn & Gillott 1974b).

The two-year life cycle of *A. colensonis* at Lake Sarah - tb represents the first report of a lestid that requires more than one year to complete development. However, *A. colensonis* probably has a one-year life cycle in other areas within New Zealand. For example, Barclay (1966) found that larvae completed development and emerged from a temporary pond between the time that the pond first filled (early June) and the time that it dried out (mid-November). Presumably eggs present in the vegetation hatched after the pond filled and some larvae completed development within five months (emergence started by late October). Barclay concluded that *A. colensonis* belonged to an ecological group that had fast developing aquatic stages of a duration short enough to enable emergence before the pond dried out. In the present study, the cooler winters and lower temperatures experienced during the summer at Lake Sarah - tb (than at Barclay's study site) probably slowed rapid growth and caused the two-year life

cycle.

Lestids appear to be well adapted to life in temporary ponds. They are tolerant of the extreme temperature regimen experienced in such sites and possibly require relatively high temperatures for maximum growth rates. Perhaps studies of other lestid species from temperate latitudes in habitats experiencing a temperature regimen similar to that of Lake Sarah - tb will reveal additional cases of semivoltinism.

The final objective of this thesis was to examine the means by which seasonality was maintained by the various species. As specified in section 1. this study was concentrated on *X. zealandica*; however, some information was obtained on the development of the eggs and the larvae of *A. colensonis* and *P. smithii* and the eggs of *P. grayi* as well. These results were commented on in sections 6. & 7., but a more detailed comparison with previous work is made here. Finally the similarities in the patterns of seasonality between the species studied are identified, and discussed in relation to the success of adaptations to the New Zealand climate.

Incubation of the eggs at temperatures above 9-12°C resulted in direct development of *X. zealandica* and *P. grayi*, whereas an indication of delayed hatching was shown for *A. colensonis*. The eggs of *P. smithii* entered diapause at temperatures below 19-20°C, but developed directly at higher temperatures. Direct development probably is observed more frequently in odonate eggs than the other types of response and is discussed first. It has been noted previously in species belonging to the three families examined during the present study. These studies include those made on:

- the Coenagrionidae by Parr (1970), Sawchyn & Gillott (1975), Rivard *et al.* (1975) and Ingram & Jenner (1976b);
- the Lestidae by Lutz & Pittman (1968) and Ingram (1976b); and
- the Corduliidae by Lieftinck (1933), Fraser (1951) and Kormondy (1959).

In *X. zealandica* and *P. grayi* the embryos eventually died or the eggs failed to develop at temperatures below 9-12°C. In the only studies carried out over a range of temperatures on species showing direct embryonic development a similar, relatively high temperature requirement for development was found for the eggs of *E. boreale* by

Rivard *et al.* (1975) and for the eggs of *Leucorrhinia intacta* Hagen by Deacon (1975). The former species experienced high mortality at temperatures below 15 to 17°C and the latter species died when incubated at temperatures below approximately 13°C. Also, the eggs of *Coenagrion angulatum* Walker and *Coenagrion resolutum* Hagen showed a considerable decrease in the rate of development at 16°C compared with 21°C (Sawchyn & Gillott 1975). Possibly at slightly lower temperatures these eggs may fail to hatch. Perhaps this requirement of relatively high temperature for successful completion of the egg stage is a characteristic of the odonate species that show direct embryonic development. Usually the eggs develop rapidly and hatch the summer that they are laid, while temperatures remain relatively high. Because the eggs fail to develop when exposed to cool conditions, they are incapable of surviving the winter. Therefore, oviposition has to take place well before the onset of cold weather if the eggs are to hatch.

In *X. zealandica* the seasonal emergence of at least 90% of the emerging cohort usually was completed by mid-February at Isaac's Pond and both the Lake Sarah sites (Fig. 28). This timing of the end of emergence provided adequate time for most of the adults to mature and reproduce before the onset of cold weather. The preferred oviposition site appeared to be floating or submerged vegetation in shallow water. During warm, sunny days in the autumn the eggs in these sites possibly received sufficient exposure to temperatures above 9-12°C to complete development and to hatch.

Seasonal emergence of *P. grayi* ended by late January at Lake Sarah - 1s (Fig. 44) which probably provided a sufficient period of warm conditions during February, March and sometimes April for the maturation of adults, reproduction, and completion of development and hatching of the eggs. Although oviposition took place over weed banks in deep water at the centre of Lake Sarah, the eggs probably experienced relatively high temperatures near the surface. Armstrong (1958a) found that the gelatinous membrane surrounding *P. grayi* eggs expanded on contact with water and became very sticky. At Lake Sarah the eggs probably adhered to the vegetation near the surface of the water and, therefore, experienced conditions similar to those described for *X. zealandica*. Both *X. zealandica* and *P. grayi* apparently oviposit in a manner such that the cold intolerant egg stage is likely to complete embryonic development and hatch before the onset

of winter.

Unlike the above species, *A. colensonis* showed delayed hatching (possibly some form of diapause) as well as direct development in the egg stage. Among the Lestidae, a well defined diapause state has been shown previously in *L. sponsa* (Corbet 1956b), *L. disjunctus disjunctus*, *L. unguniculatus*, *L. dryas* and *L. congener* (Sawchyn & Church 1973) and possibly in *L. disjunctus australis* and *A. grandis* (Ingram 1976b). The embryos of *L. sponsa* completed blastokinesis and reached an advanced stage of morphological development in which they spent the winter (Corbet 1956b). Three of the four species studied by Sawchyn & Church (1973) also showed a pattern of development similar to the above; only *L. congener* entered diapause in a stage immediately before blastokinesis. The eggs of all these species hatched during the spring, after a long exposure to cool conditions. Both Corbet and Sawchyn & Church found that 10°C was the optimum temperature for the completion of diapause. A second phase of embryonic development, controlled by photoperiod, was also noted in *L. disjunctus* and *L. unguiculatus* (Sawchyn & Church 1973).

The embryonic development of *A. colensonis* differed considerably from the above. Most eggs hatched directly without previous exposure to low temperatures and the eggs developed in a similar manner at the LD or SD photoperiods. Previously, Peterson (unpublished report, Zoology Department, University of Canterbury, Christchurch, September 1976) suggested that short day photoperiods had an inhibitory effect on the embryonic development of *A. colensonis*. She exposed eggs to a long day photoperiod (16L:8D) and complete darkness (0L:24D). Temperatures varied between 18 and 26°C, especially in the former conditions where fluctuations were caused mainly by the lighting. In her experiments fewer eggs hatched in the 0L:24D than in the 16L:8D light conditions. In the present study no differential response by the eggs was observed when kept at the natural LD (16L:8D) and SD (10L:14D) photoperiods, held at a relatively constant temperature (approximately 19-20°C) (section 6.5.3.). Perhaps the response observed by Peterson was caused by the unnatural photoperiod (0L:24D) and/or the difference in temperatures experienced between the two groups because of the lighting.

In the present study a delayed hatching of eggs occurred that was not related to the photoperiod regimens experienced. This delayed hatching, however, did not ensure that it was the egg stage that overwintered because, at a maximum, only approximately 24% of the eggs showed this response. Further interpretation of delayed hatching

cannot be made at present because of insufficient information about the nature of this response.

The high mortality (about 75%, see pp. 114 & 115) that was experienced during the winter at Lake Sarah - tb possibly indicated that the egg stage was not suited to withstand cold conditions. Perhaps the egg stage of *A. colensonis* is better suited to survive periods of drought rather than to survive the winter. For example, Barclay (1966) noted that *A. colensonis* larvae of an unspecified size were present in a temporary pond near Auckland, New Zealand, about one month after it filled with water in June. Few, if any, adults are present at Auckland during June (R. Rowe, Zoology Department, University of Canterbury, Christchurch, pers. comm. 1979); so that the larvae probably did not hatch from eggs laid after the pond filled with water. A likely alternative is that the eggs were laid earlier than June and that they remained viable in the stem and were protected against dessication during the period when the pond was dry. Subsequently the eggs might have hatched after the pond filled with water.

The above supposition that *A. colensonis* eggs are drought-resistant is similar to that made by Corbet (1962, p.34), concerning the drought-resistant eggs of certain tropical odonates. *A. colensonis* may have an egg stage in which hatching is triggered by sufficient wetting; however, this has not been confirmed experimentally. If it is the case then the egg stage of *A. colensonis* is an adaptation better suited as a means to survive periods of drought in temporary ponds than as a means to survive the winter in temperate areas.

The last egg response to be discussed is that of *P. smithii*. The unusual diapause response of the eggs that apparently was induced by temperatures below 19-20°C, has not previously been recognised in the Odonata. Unfortunately, because of the provisional nature of the results obtained, a detailed comparison of this type of diapause with others reported in the Odonata (pp. 71-74, Ando 1962) is unjustified at this time. Further work on this topic is strongly recommended.

There is little information on the egg response of corduliids for comparison with the response that was shown by *P. smithii*. Lieftinck (1933) found that the eggs of *Procordulia artemis* Lieft. developed directly, as was also found for *T. cynosura* (Kormondy 1959) and for *P. grayi* in the present study. Direct development of corduliid eggs possibly occurs frequently; however, some evidence exists which suggests that the response shown by *P. smithii* is not an isolated

occurrence within the Corduliidae.

During casual observations of eggs from one female of *Oxygaster curtisii* (Dale), Fraser (1951) found noticeable differences in the response of eggs set up in various conditions. One group that was kept in a warm room hatched in 24 days, whereas a second group that was kept in cooler conditions in the "open" required about 72 days to hatch. He concluded that the wide variation in the incubation period was caused by the difference in the temperature regimens experienced by the eggs. Although no temperature records were kept, Fraser mentioned that a "hot spell" of weather was prevalent during the study. The eggs were collected during summer on 3 July, in Hampshire, England.

In the above study, perhaps the temperatures experienced in the warm room exceeded a mean of 20°C, whereas those experienced in the "open" were only slightly lower because of the "extremely hot and almost tropical weather" that prevailed. The incubation periods of the *O. curtisii* eggs were remarkably similar to the response of *P. smithii* eggs kept at 20°C (22 days, Table 20) and at 19.1°C (64 to 72 days, Table 19). It can be speculated that the observations made by Fraser (1951) possibly indicate a response to temperature by *O. curtisii* eggs which is similar to that of *P. smithii*.

Another corduliid that shows an unusual egg hatching is *Somatochlora viridiaenea viridiaenea* Uhler. Miyakawa (1971) found that eggs from one female showed a distinct bimodal hatching pattern during a six-month incubation period. This bimodal hatch indicates two rates of development of the eggs, perhaps similar to the response noted for *P. smithii* in this study (Fig. 48).

Neither of the above studies specifically examine the effects of temperature on egg incubation; however, they do show the occurrence of direct and prolonged (possibly diapause) rates of development of eggs from the same batch which, at least in the case of *O. curtisii*, may be induced by temperature. Perhaps a temperature induced diapause, as in *P. smithii* occurs more frequently than previously suspected. Further observations, especially on the eggs of corduliids, must be made to ascertain the nature of this response.

One of the main factors regulating the seasonality of the species studied was the threshold temperature for development of the larvae. The effect of this was shown clearly by the difference in the duration of the life cycle of *X. zealandica* at Isaac's Pond (two years) and at Lake Sarah - tb (three years). The threshold temperature for development of the later instar larvae (F-2 to F) of *X. zealandica*

fell between 7 and 9°C (section 7.3.1.); therefore, during the winter development continued at Isaac's Pond, whereas development ceased at Lake Sarah - tb.

The threshold temperature for development of the F-1 and F instar larvae of *A. colensonis* (8-12°C) was slightly higher than that of *X. zealandica*; however, development probably still continued during the winter at Isaac's Pond, whereas it stopped at Lake Sarah - tb. Because relatively few *A. colensonis* larvae were obtained at Isaac's Pond a continuation of growth during the winter was not confirmed by the larval survey, although the earlier start of emergence from this site than from Lake Sarah supported this inference.

Prior to this work, the threshold temperature for development was reported for only two other odonates. Trottier (1971) calculated from laboratory experiments that the threshold temperature for development of F instar larvae of *Anax junius* Drury was about 9°C. Also based on laboratory experiments, the threshold temperature for development of the F-1 and F instar larvae of *L. intacta* was calculated to be approximately 8 to 10°C (Deacon 1975). In addition to the above, a possible third record, indicating the threshold temperature for development of *Ischnura elegans* (van der Linden) has been reported. Thompson (1978) found that a population of *I. elegans* stopped growth in the field at about 8°C. In the laboratory, he found that the larvae showed a low attack (feeding) rate below this temperature and, therefore, concluded that growth stopped in the field because feeding was possible, but low below 8°C. This temperature probably is reasonably close to the threshold temperature for development as well. Overall, these observations indicate a possible trend towards a threshold temperature for development of odonates from temperate regions of about 7 to 12°C; however, this suggestion is based only on a small amount of information and must be treated with reserve.

The threshold temperature for development may prove useful in establishing the temperature limits for the range of species. For example, because *X. zealandica* has a lower threshold temperature for development than *A. colensonis*, it may be better adapted for life in cooler habitats. Therefore, *X. zealandica* can be expected to occur at higher altitudes or in cooler springs, lakes and rivers, than *A. colensonis*. Based on personal observation this type of distribution does appear to be the case in New Zealand. Crumpton (1977) in a report on the Odonata distribution in Canterbury and Westland also

noted that *A. colensonis* was found at Lake Sarah (579m) and that *X. zealandica* was found up to 915 to 924m. However, the above suggestion that *X. zealandica* can occur in cooler habitats than *A. colensonis* is tentative and must be treated with reserve.

Although *X. zealandica* had a lower threshold temperature for development, than *A. colensonis* at Lake Sarah - tb, it had a three-year life cycle, whereas *A. colensonis* had a two-year life cycle. This difference in voltinism was probably related to the difference between the two species in the number of degree days required to complete development in corresponding instars or stages (see Tables 22 & 23). *X. zealandica* has a higher degree day requirement than *A. colensonis* (perhaps in all the instars); therefore, *X. zealandica* has a longer life cycle. *A. colensonis* probably is better adapted for rapid development in warmer habitats, whereas as mentioned earlier, *X. zealandica* may be better adapted for life in cooler habitats.

The principal means by which seasonality was maintained in the species studied probably was through a growth restriction in the larval stage(s). Various aspects of this growth restriction in *X. zealandica* were described and discussed in detail earlier (section 7.3.4.) when it was concluded to be a form of diapause. The nature of this diapause is re-examined here in relation to previous work on diapause in the Odonata. The growth restrictions noted in *A. colensonis* and *P. smithii* are not discussed because of insufficient information.

In Odonata, diapause was first investigated in *A. imperator* (Corbet 1956a). This work stimulated an interest in this research topic and subsequently a diapause response or prolonged development was found in larvae of many odonate species. Overall, the response varies considerably from species to species. The principal findings from previous works show that at least three environmental factors are concerned in the regulation of diapause or prolonged development. Firstly, a long day photoperiod may promote a higher growth rate in larvae than a short day photoperiod (p.196). Secondly, the period of the autumnal equinox can be associated with the occurrence of major developmental events during the larval stage. For example, in some species a reversal in the response of larvae to photoperiods occurs (p.197) (*i.e.*, long day lengths prolong development before the equinox, whereas short day lengths prolong development afterwards) and/or in other species moulting into the F instar is stimulated by equinoctial photoperiods (p.197). Thirdly, diapause is completed in

less time if the larvae are exposed to cool conditions (approximately 10°C) and/or a short day photoperiod for a given length of time before transferral to relatively warm conditions and a long day photoperiod (p. 198). These three factors are discussed now and related to the responses shown by *X. zealandica*.

Jenner (1959) found that a long day photoperiod (13 or 14 hours of light per 24-hour day) promoted the larval development of the odonates tested compared with the developmental rates in a short day photoperiod (11L:13D). Similar reports were made for several species by Macklin & Montgomery (1962), Jenner (1963), Montgomery (1963), Lutz (1968b) and Shepard & Lutz (1976) which indicated that a growth response to day length differences possibly was widespread. However, as mentioned earlier, a reversal in response to photoperiod occurs centred around the autumnal equinox. In all of the above studies either the experiments were started after the equinox or larvae in the instars tested were absent from the population until after that time. Perhaps if experiments had been started before the autumnal equinox then a long day induced developmental delay would have been noted.

Of course, factors other than day length could affect growth rates to cause this apparent response to photoperiod. For example, if larvae feed for a longer period in the longer day length (*i.e.*, food is available longer) then possibly the rate of development of larvae in these conditions is higher also. Alternatively, if larvae in the long day photoperiod experience a warmer temperature regimen because of incident heat from the lighting then this could cause a difference in growth rates between the larvae in the different photoperiod conditions. However, in the above studies, Jenner (1963) ascertained that the feeding of the larvae remained independent of photoperiod and the experiments by Lutz (1968b) and Shepard & Lutz (1976) were carried out in adequately controlled equipment in which the temperature regimen remained independent of photoperiod. Therefore, neither food availability nor temperature appeared to be the critical factors that caused the differential response of the larvae. Perhaps, as suggested, the apparent long day promotion of growth may be an artifact caused by the timing of experiments. This possibility illustrates the necessity for continuing experiments of this nature throughout the year.

No consistent LD promotion of development was noted in the present study on *X. zealandica*, either before or after the autumnal equinox. Larvae in the instars tested entered diapause regardless of the fixed photoperiod, although the intensity of this response was affected by photoperiod, but not in the same manner for all the instars. Before the autumnal equinox, F instar larvae showed a strong prolonged response to the SD photoperiod; F-1 instar larvae showed a strong prolonged response to both photoperiods during January and to the LD photoperiod up to the time of the equinox; and F-2 instar larvae showed the same response to both photoperiods up to the time of the equinox (see p.169).

After the autumnal equinox, F and F-1 instar larvae showed a weak response to both photoperiods, whereas F-2 instar larvae showed no differential response to the photoperiods (see p.170). Therefore, although the LD photoperiod was not observed to promote development in *X. zealandica*, major developmental events did occur at the time of the autumnal equinox.

The above major developmental events, centred around the autumnal equinox, did not include a reversal in the response of larvae to photoperiod. This response (see earlier, p.195) was first observed in *T. cynosura* (Lutz & Jenner 1964) and later examined in detail in the same species by Lutz (1974a, 1974b). Other species reported to respond in this manner are: *Aeshna viridis* Eversm. (Norling 1971); *L. intacta* (Deacon 1975); *L. dubia* (Norling 1976); and *E. aspersum* (Ingram & Jenner 1976a). A two-step photoperiodic reaction appears to be widespread within the Arthropoda (Zaslavsky 1972) and may occur more frequently in the Odonata than previously indicated. *X. zealandica*, however, did not respond in this manner (see summary of photoperiodic responses listed above).

As mentioned earlier, another event centred around the autumnal equinox that occurred in some species is the entry into the F instar. One of the first observations of this event was that larvae of *A. imperator* moulted into the F instar near the time of the equinox (Corbet 1956a). This restricted moult into the F instar was later reported for *T. cynosura* (Lutz 1974a) and also was noted for *X. zealandica* during this study; however, in the former case Lutz suggested that the moult was in response to decreasing photoperiods of less than 12 hours day length, whereas in the latter case the moult probably occurred because diapause ended in the F-1 instar larval

population, possibly in response to the decrease in the rate of change of day length.

Compared with *A. imperator* (Corbet 1956a) and *T. cynosura* (Lutz 1974a), the moult of *X. zealandica* into the F instar occurred during a longer period centred around the equinox. Some of the larvae moulted into the F instar before the autumnal equinox, especially at Lake Sarah - tb, where F-1 instar larvae were able to complete diapause before receiving the optimal photoperiodic cue (probably the equinoctial photoperiods). This response was thought to be related to the difference between voltinism of *X. zealandica* at Isaac's Pond and Lake Sarah - tb. The F-1 instar larvae at the latter site appeared in the new cohort earlier during the year than at Isaac's Pond, and therefore, some larvae completed diapause before the equinox because they were exposed to relatively warm conditions for a longer period.

Corbet (1956a) suggested that exposure to a temperature of about 10°C followed by relatively warm conditions was essential for a rapid completion of diapause in the larvae of *A. imperator*. He proposed that diapause was completed in nature by late autumn (November), at a time when metamorphosis was not possible because temperatures were already too low.

Similarly, Ingram (1975) found that diapause of *E. hageni* and *E. aspersum* larvae was completed after exposure to either low temperatures (10°C) or short day lengths followed by transferral to relatively warm conditions. These larvae remained responsive to photoperiod until late winter (February) and showed supplementary (extra) moulting at short day lengths and relatively high temperatures (Ingram & Jenner 1976a). Both of these responses ensured that emergence during the late autumn was prevented.

In the present study exposure to low temperatures was unnecessary for the completion of diapause in the F-2 and F-1 (strong response) instar larvae of *X. zealandica*. Diapause was terminated probably by the rate of change of day length, except in the F instar larvae which appeared to require exposure to cool conditions as well (see pp.170 & 171). The weak diapause response also appeared to be terminated by exposure to low temperatures (see p.171). This sequence of responses effectively prevented emergence during the late autumn.

In view of the above discussion the nature of the diapause of *X. zealandica* is unusual when compared with the diapause described for other species. Long day lengths do not promote development either before or after the autumnal equinox (see pp.169 & 170); there is no reversal in the response of larvae to photoperiod centred around the equinox (see pp.169 & 170); and (except for the F instar and the weak diapause response) diapause appears to be terminated by changing day lengths (see pp.170 & 171).

The features of diapause shared by *X. zealandica* with other species are few. The moult into the F instar at the time of the equinox and the requirement for cool conditions for the completion of the strong diapause response in the F instar larvae and the weak diapause response in the F and F-1 instar larvae were the only features noted. In spite of this response the effect was similar; emergence was prevented during the autumn as in *A. imperator* (Corbet 1956a), *E. hageni* and *E. aspersum* (Ingram & Jenner 1976a).

In *X. zealandica*, *A. colensonis*, *P. smithii* and *P. grayi* emergence during the late autumn would probably contribute little towards the continuation of the species. Although conditions often remain warm until late April or even May at Isaac's Pond, the weather is variable at that time of the year and cold periods sometimes occur during March. In most of the species studied over 90% of the population completesemergence by late February (Figs. 28, 37 & 44). This probably allows a sufficient period for the completion of maturation of the adult, mating, oviposition and, in the case of *X. zealandica*, the successful hatch of the cold-sensitive eggs.

The seasonality of these odonates within Mid Canterbury is such that emergence is avoided at a time of the year when successful reproduction is unlikely. Although New Zealand enjoys a relatively mild climate compared with other areas at similar latitudes, the odonate species studied show some adaptations that are suited for life in cooler climates at higher latitudes.

ACKNOWLEDGEMENTS

I thank Ann Jensen for her help with the field and laboratory work, the figures and especially for her helpful comments on the manuscript.

My supervisors were P.S. Corbet, V.M. Stout

Comments on the manuscript were given by P.S. Corbet, A. Jensen and V.M. Stout.

Assistance with the field and laboratory work was obtained from S. Deacon, E. Fordyce, A. Jensen, R. McCammon and R. Ogilvie. Advice on statistics was provided by K. Duncan. Plant identifications were made by A.T. Dobson. Material for the experiments in section 6.6.2. was collected by R. Rowe. Technical help was received from J. Buckley, A. Gall, J.T. Kay, R.H. Thompson and T.P. Williams.

Entertaining evenings were provided by M. McGlone. My squash partner was P. Davie and my stalwart cycling companions were E. Fordyce, A. Jensen and J. Lowry.

The final draft of this thesis was typed by Val Goulding.

I thank the Isaac family for unrestricted access to Isaac's Pond.

This work was supported by a New Zealand University Grants Committee Commonwealth Scholarship.

Finally, I make special mention of the encouragement received from A. Jensen, U. Norling and V.M. Stout.

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